



Gymnosporangium species on *Malus*: species delineation, diversity and host alternation

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Key words

Apple rust
host alternation
new taxa
species delimitation

Abstract *Gymnosporangium* species (*Pucciniaceae*, *Pucciniales*, *Basidiomycota*) are the causal agents of cedar-apple rust diseases, which can lead to significant economic losses to apple cultivars. Currently, the genus contains 17 described species that alternate between spermogonial/aecial stages on *Malus* species and telial stages on *Juniperus* or *Chamaecyparis* species, although these have yet to receive a modern systematic treatment. Furthermore, prior studies have shown that *Gymnosporangium* does not belong to the *Pucciniaceae* sensu stricto (s.str.), nor is it allied to any currently defined rust family. In this study we examine the phylogenetic placement of the genus *Gymnosporangium*. We also delineate interspecific boundaries of the *Gymnosporangium* species on *Malus* based on phylogenies inferred from concatenated data of rDNA SSU, ITS and LSU and the holomorphic morphology of the entire life cycle. Based on these results, we propose a new family, *Gymnosporangiaceae*, to accommodate the genus *Gymnosporangium*, and recognize 22 *Gymnosporangium* species parasitic on *Malus* species, of which *G. lachrymiforme*, *G. shennongjiaense*, *G. spinulosum*, *G. tiangkengense* and *G. kanas* are new. Typification of *G. asiaticum*, *G. fenzelianum*, *G. juniperi-virginianae*, *G. libocedri*, *G. nelsonii*, *G. nidus-avis* and *G. yamadae* are proposed to stabilize the use of names. Morphological and molecular data from type materials of 14 *Gymnosporangium* species are provided. Finally, morphological characteristics, host alternation and geographical distribution data are provided for each *Gymnosporangium* species on *Malus*.

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INTRODUCTION

Plant parasitic rusts within the order *Pucciniales* represent one of the largest groups of fungal plant pathogens, which occur on ferns to advanced monocots and dicots (Aime 2006, Webster & Weber 2007). Approximately 7800 rust species are currently recognised worldwide, with many species causing significant economic losses to agricultural or forest crop plants (Arthur 1934, Hiratsuka et al. 1992, Cummins & Hiratsuka 2003). Among them, cedar rusts are one of the most important genera of phytopathogens (Helfer 2005). These pathogens belong to the genus *Gymnosporangium*, which previously has been placed in the family *Pucciniaceae* (*Pucciniales*, *Basidiomycota*), and are obligate biotrophic phytopathogens (Cummins & Hiratsuka 1983, 2003). Presently over 64 species have been recorded, having a demicyclic (macrocytic or microcytic in a few species) life cycle with a telial stage on gymnosperm trees in *Cupressaceae*, and an aecial stage on trees of the apple tribe, *Maleae*, in the family *Rosaceae* (Kern 1973, Shen et al. 2018, Farr & Rossman 2019).

Within the genus *Gymnosporangium*, cedar-apple rusts represent some of the most serious and devastating diseases occurring in apple plantations worldwide (Sinclair & Lyon 2005, Zhao et al. 2016, Lâce 2017). They occur on leaves, fruits and stems

of *Malus* species, cause premature defoliation, and eventually kill their hosts plants (Helfer 2005). Hitherto, up to 17 *Gymnosporangium* species are known as causal agents of apple rust diseases, having mostly been reported from temperate regions in Asia, Africa, Europe and North America (Farr & Rossman 2019). Eleven *Gymnosporangium* species have been reported on 16 *Malus* species and their hybrids in Asia (Azbukina 1972, Wang & Guo 1985, Hiratsuka et al. 1992, Zhuang et al. 2012), and nine *Gymnosporangium* species have been reported on 17 *Malus* species and their hybrids in North America (Arthur 1934, Ziller 1974). Six *Gymnosporangium* spp. have been reported on *M. baccata*, *M. domestica*, *M. pumila* and *M. sylvestris* in Europe, and only one *Gymnosporangium* species has been reported from Africa (Hylander 1953, Jørstad 1962, Wilson & Henderson 1966, Farr & Rossman 2019). Among them, *G. asiaticum*, *G. clavipes*, *G. globosum*, *G. juniperi-virginianae* and *G. yamadae* are listed as quarantine pests in Asia, Europe, and North America (Duan et al. 2017, EPPO 2017, 2018). Accurate and efficient species recognition, as well as a better understanding of their life cycle are thus important for plant quarantine and effective disease control.

Traditional taxonomy of *Gymnosporangium* relies on morphological distinctions in spermogonia and teliospores at generic and suprageneric level, and this genus has long been placed in *Pucciniaceae* (Dietel 1928, Cummins & Hiratsuka 1983, 2003). However, recent molecular studies revealed a phylogenetic distinction of *Gymnosporangium* from other members of the *Pucciniaceae* (Maier et al. 2003, Wingfield et al. 2004, Aime 2006) but did not conclusively resolve the relationship of *Gymnosporangium* within other recognized families in the order *Pucciniales*. Species recognition relies on the morphology of known spore stages, i.e., the telia or aecia occurring on different host species (Kern 1908, 1973, Sydow & Sydow 1915, Hiratsuka et al. 1992, Cummins & Hiratsuka 2003). Host

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specificity is generally also employed for species recognition (Sydow & Sydow 1915, Kern 1964, Parmelee 1971). However, due to their diverse life cycles, overlapping host ranges, and lacking uredinial stages in most species, considerable disagreements on species delimitation still exist (Kern 1970, Peterson 1982, Novick 2008). In addition, several morphological characteristics in aecial or telial stages have been employed as important criteria in distinguishing species, but their phylogenetic significance has not been evaluated. Thus, previous reports of 17 *Gymnosporangium* species on *Malus* species remain dubious due to the lack of a consistent species concept. Our previous studies have shown that the recognition of all spore stages is essential for species recognition (Zhao et al. 2016). Nevertheless, the connection between aecial and telial stages and the characterisation of holomorphic morphology remain unknown for most species.

In this study, comprehensive morphological and molecular studies were conducted among rusts occurring on *Malus* and their potential alternate hosts. The objectives of the current study were:

1. to determine the phylogenetic placement of *Gymnosporangium* in the order *Pucciniales* (*Basidiomycota*);
2. to clarify the species boundaries of *Gymnosporangium* species on *Malus*;
3. to confirm the connection of potential alternate hosts of *Gymnosporangium* where possible;
4. to describe the taxonomic novelties based on molecular phylogeny and morphology.

MATERIALS AND METHODS

Materials examined in this study

A total of 464 dried fungarium specimens were examined from different herbaria to cover the largest possible *Malus* host species distribution based on published taxonomic literature (Kern 1973, Farr & Rossman 2019). Specimens with either aecial or telial stages were chosen according to the name on the attached labels and their host information. Among them, 186 specimens were on the telial hosts *Juniperus* and *Libocedrus* species, and 242 specimens were on *Malus* species and other related hosts. Fungarium specimens were loaned from the following fungaria: The Mycological Herbarium of Institute of Microbiology, CAS, China (HMAS); Plant Pathology Herbarium, Cornell University, Ithaca, New York, USA (CUP); New York Botanical Garden, New York, USA (NYBG) and New York State Museum, New York, USA (NYS). To supplement fungarium material, 36 fresh collections were also included. Among these 464 specimens, type specimens of the following species were included for comparative studies: *G. aurantiacum*, *G. betheli*, *G. biseptatum*, *G. connersii*, *G. distortum*, *G. exterum*, *G. fenzeilianum*, *G. fraternum*, *G. gracile*, *G. haraeaeum*, *G. japonicum*, *G. kernianum*, *G. nelsoni*, *G. nidus-avis* and *G. yamadae*.

Molecular phylogeny and species delimitation

Several rust sori were excised from each specimen and DNA was extracted by means of a Genra Puregene Tissue Kit (Qiagen, Valencia, CA) according to the manufacturer's instructions. For some old fungarium specimens, DNA extraction was diluted 50–100-fold to successfully amplify the target fragment. To study the phylogenetic position of each taxon, three nuclear ribosomal RNA gene regions, the internal transcribed spacer regions and intervening 5.8S nrRNA gene (ITS), the large subunit (LSU) and the small subunit (SSU) rDNA were amplified, and a nested PCR method was employed to improve the amplification. Detailed information of primers and annealing temperatures of these target fragments followed that of Zhao et al. (2016).

To clarify the phylogenetic placement of the genus *Gymnosporangium*, sequences of rDNA SSU-ITS-LSU from 703 representative taxa belonging to 77 genera within the order *Pucciniales*, which cover 14 morphologically defined families, were included for phylogenetic analyses. These representative taxa were selected based on previous phylogenetic studies as listed in Table S1. Due to alignment difficulties, ITS1 regions in all taxa were excluded from further analyses. Eight species of *Helicobasidium*, *Insolibasidium*, *Jola*, *Septobasidium* and *Tuberculina* of three orders, *Helicobasidiales*, *Platyglloeales* and *Septobasidiales* from the subphylum *Pucciniomycotina* were selected as outgroups. At species level in *Gymnosporangium*, rDNA SSU, ITS and LSU were successfully amplified from 184 fungarium specimens, and sequence data of rDNA SSU, ITS and LSU from 212 specimens of *Gymnosporangium* were retrieved from GenBank. All these specimens used for phylogenetic studies were listed in Table S2, together with their GenBank accession numbers and other information. *Endoraecium tropicum* was selected as outgroup based on phylogeny of the order *Pucciniales*. In the final alignment, raw sequence data were aligned by Bioedit v. 7.0.9 (Thompson et al. 1997), and multiple alignments were performed with MAFFT v. 7.394 (Katoh et al. 2017). SSU, ITS and LSU were combined to yield the best results for the phylogeny. Topologies were constructed based on maximum likelihood (ML) analyses using RAxML v. 0.95 (Stamatakis 2006). Bayesian Markov chain Monte Carlo (MCMC) analyses were performed using MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001), and Bayesian posterior probabilities (Bpp) were calculated. In ML and Bayesian analyses, the best-fit substitution model was estimated using Modeltest v. 3.7 (Posada & Crandall 1998).

Morphological examination

Detailed morphological characters of each loaned specimen were observed under the dissecting microscope (DM) (SMZ745, Nikko, Japan), light microscope (LM) (Axio Imager A2, ZEISS, Germany) and a scanning electron microscope (SEM) (Quanta 200, FEI™, USA) as outlined in Zhao et al. (2017). Morphological characteristics were compared with that of the type specimens, original descriptions, and other published descriptions of species involved (e.g., Kern 1908, 1973, Sydow & Sydow 1915, Arthur 1934, Kuprevich & Tranzschel 1957, Wilson & Henderson 1966, Hiratsuka et al. 1992, Lee & Kakishima 1999a, b, Yun et al. 2009). The different spore stages of rust fungi were designated by the following Roman numerals: spermogonia/spermatia (0), aecia/aeciospores (I), uredinia/urediniospores (II), telia/teliospores (III), and basidia/basidiospore (IV).

RESULTS

To clarify the phylogenetic relationship and familial placement of the genus *Gymnosporangium*, representative taxa of the *Pucciniaceae* and closely related families were included in the ML and Bayesian inference, which resulted in similar topologies. The phylogeny provides the best phylogenetic coverage of species, genera and families in *Pucciniales* to date, and up to 33 potential familial groups were recognised (Fig. 1a–e, Fig. S1). We recognised polyphyly of 14 traditional morphologically defined families within the order *Pucciniales* (Fig. 1a–e). Within the family *Pucciniaceae*, species in *Puccinia* or *Uromyces* species were clustered together in one phylogenetic group representing *Pucciniaceae* s.str. (Fig. 1a, S1). However, species in *Gymnosporangium* were found in one well-supported phylogenetic group (Bootstrap values = 1.000/90), and it was phylogenetically distinct from *Pucciniaceae* s.str. (Fig. 1a–d), although species in both phylogenetic groups had previously been classified in the *Pucciniaceae* due to morphological simi-

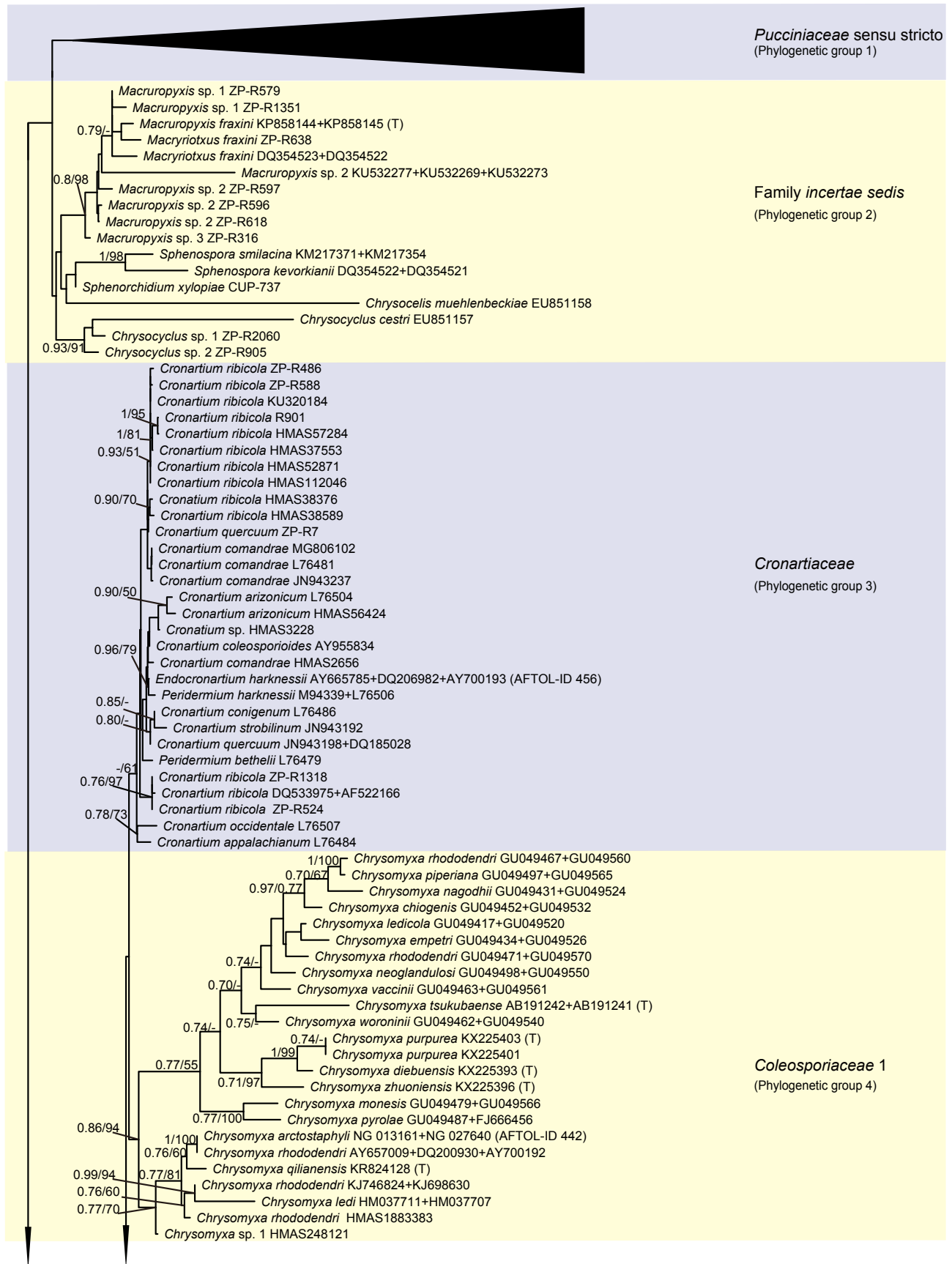


Fig. 1 Multilocus phylogenetic tree of order Puccinales based on rDNA SSU-ITS-LSU sequence data. Support values indicated at nodes. Bayesian posterior probabilities $\leq 50\%$ and Maximum Likelihood bootstrap (ML) $\leq 50\%$ were indicated by dash line (-). Family names were listed after each taxon based on Cummins & Hiratsuka (2003).

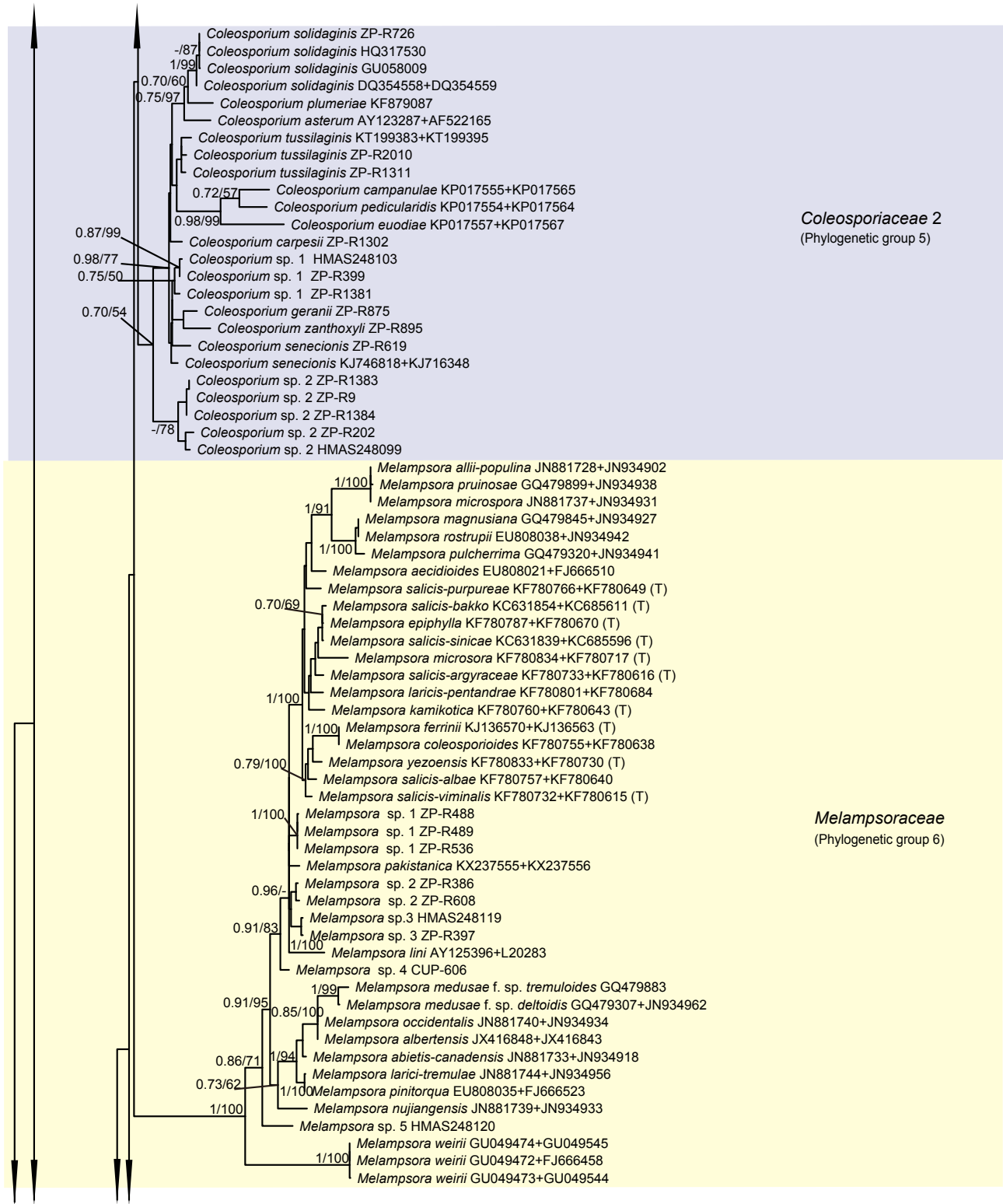


Fig. 1 (cont.)

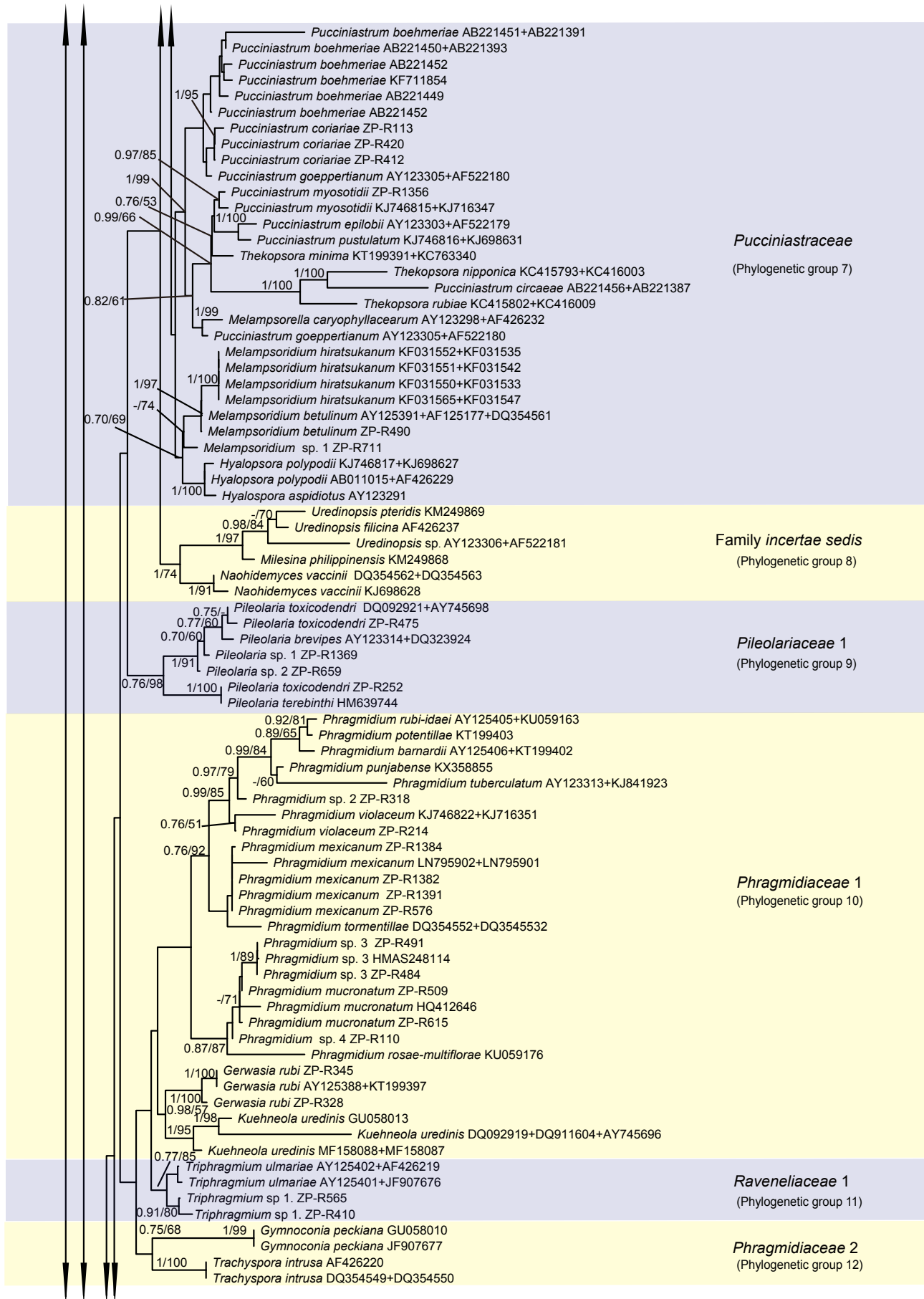


Fig. 1 (cont.)

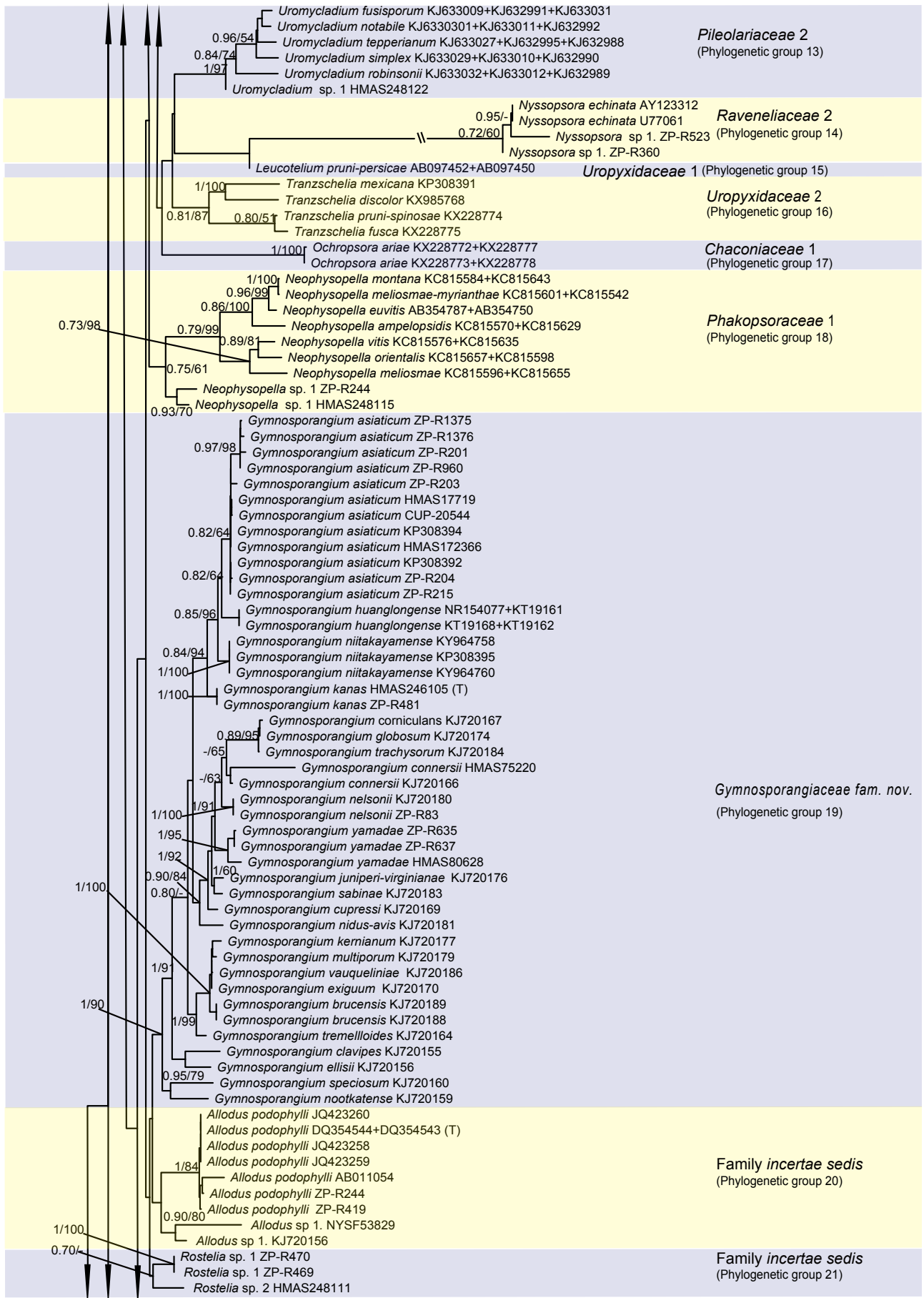


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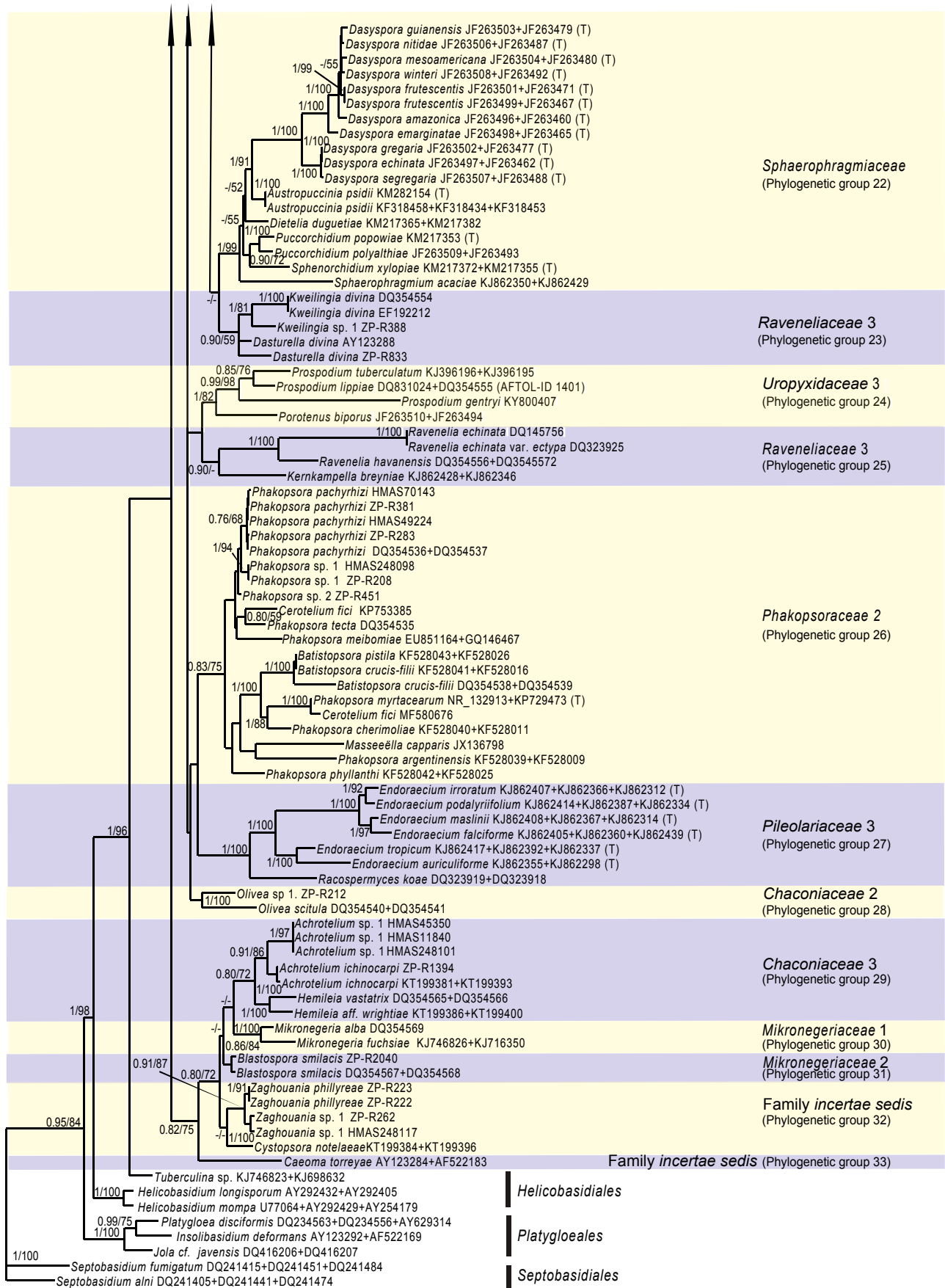


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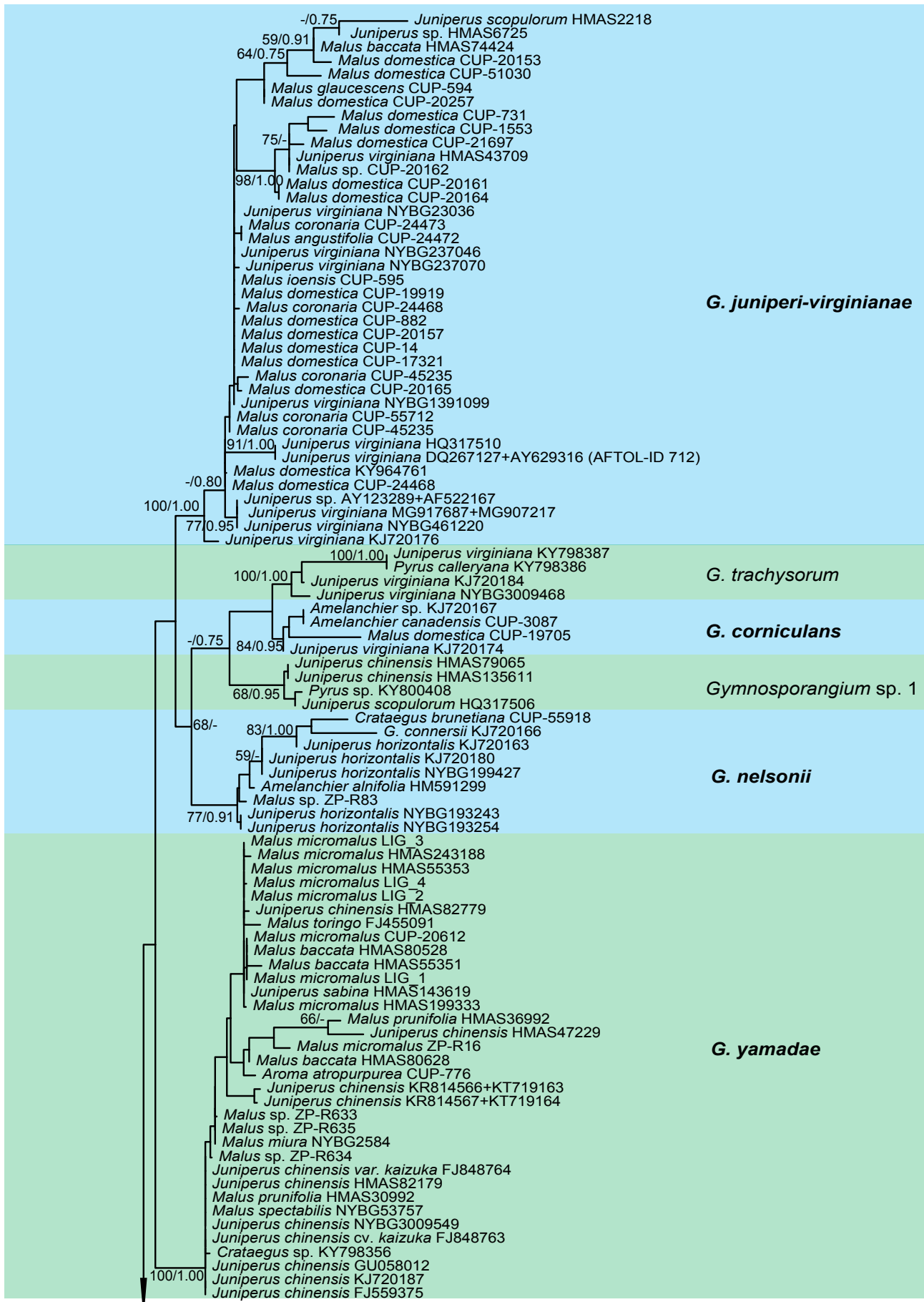


Fig. 2 Multilocus phylogenetic tree of *Gymnosporangium* species based on rDNA SSU, ITS and LSU sequence data. One of the best trees were shown and support values indicated at nodes. ML bootstrap $\leq 50\%$ and Bayesian posterior probabilities $\leq 50\%$ were indicated by dash line (-). Taxa names in **bold** represent species with their aecial hosts on *Malus* species.

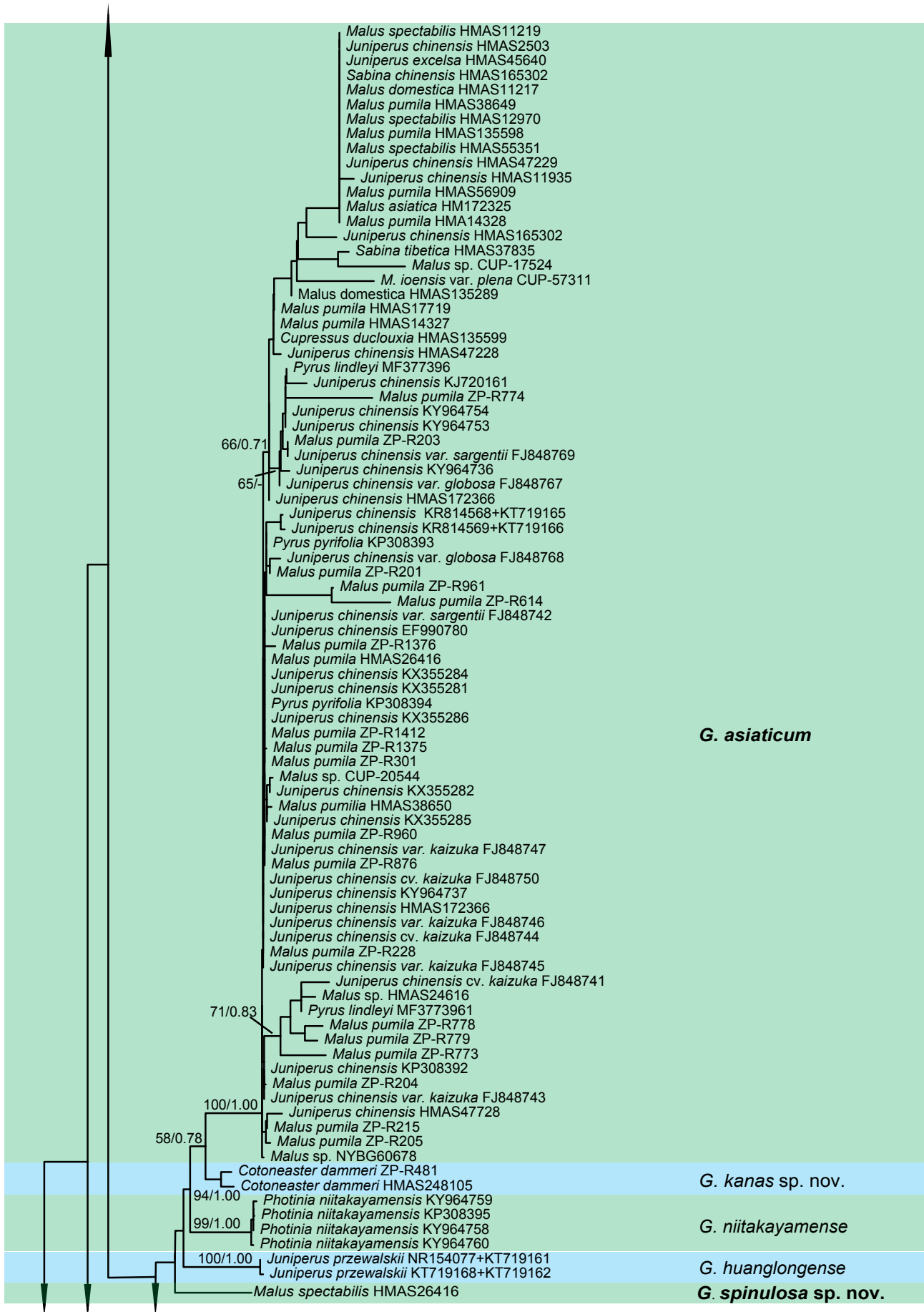


Fig. 2 (cont.)

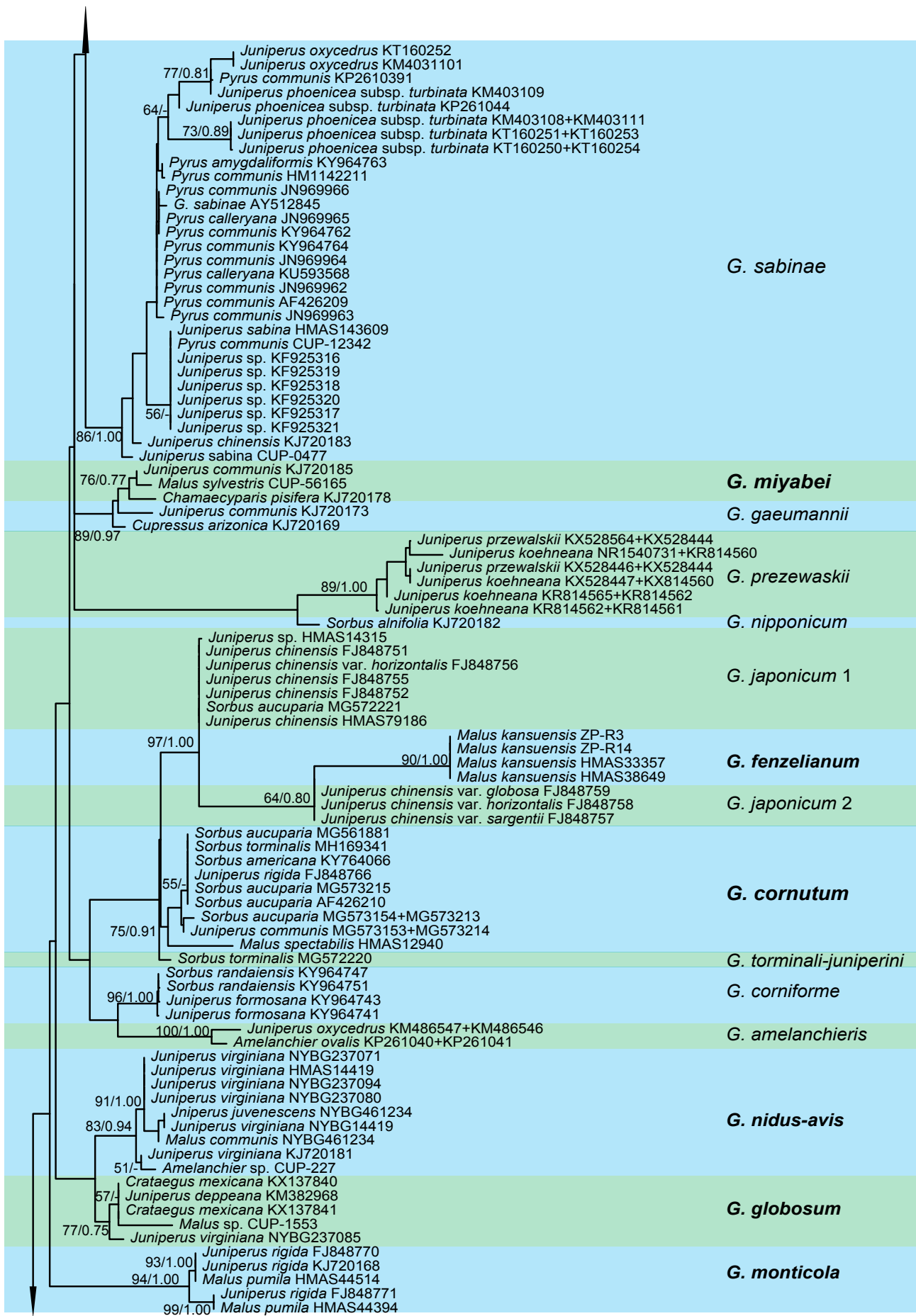


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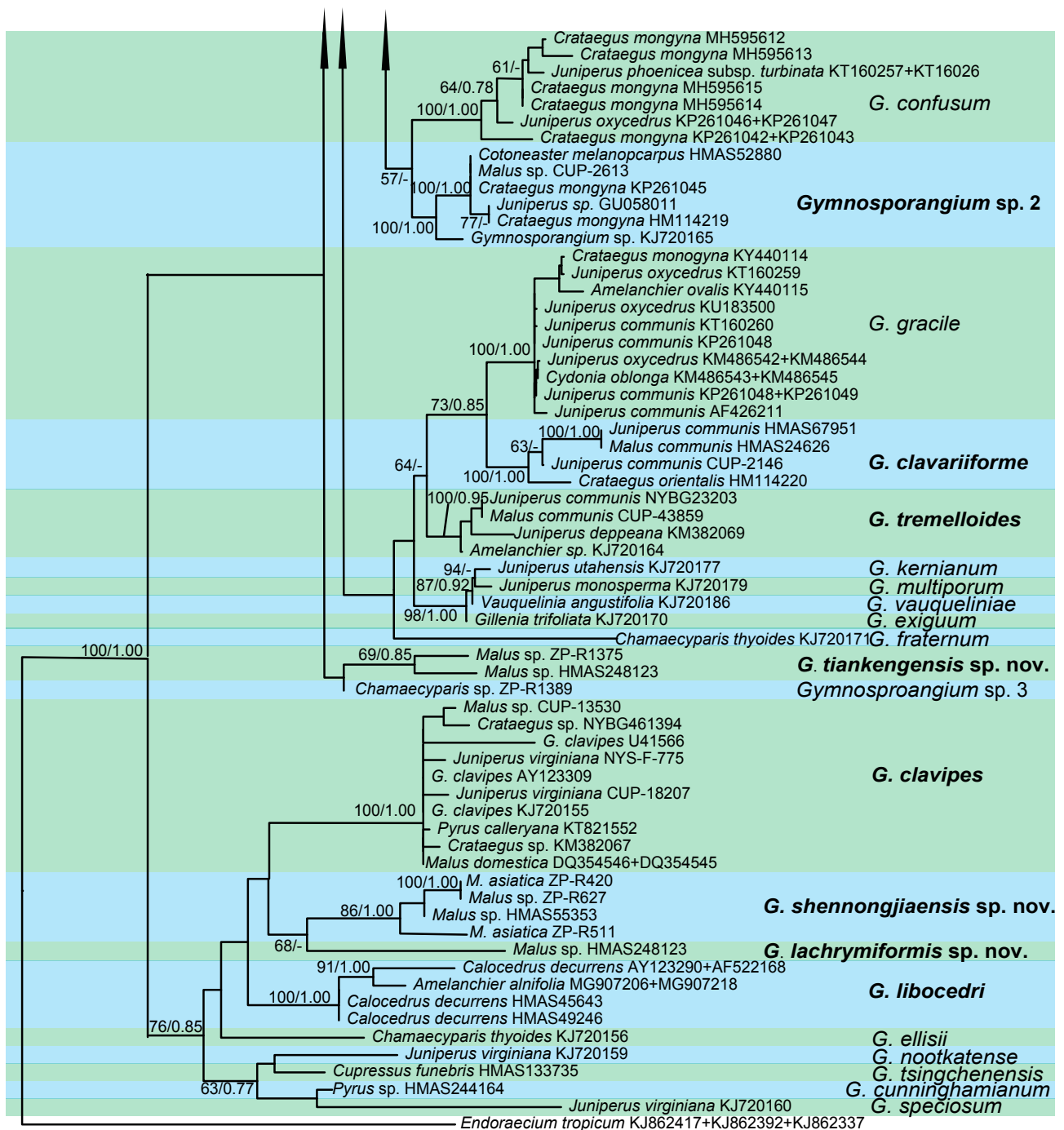


Fig. 2 (cont.)

larities in spermogonia and teliospores (Cummins & Hiratsuka 1983, 2003). *Gymnosporangium* is phylogenetically close to the Mayapple rust *Allodus podophylli* (*Pucciniales* family *incertae sedis*), *Neophysopella* (*Phakopsoraceae* sensu lato (s.lat.)) and several genera in the *Sphaerophragmiaceae* (Fig. 1d). Morphologically, *Gymnosporangium* differs from these phylogenetically related genera or families (Cummins & Hiratsuka 1983, 2003). *Gymnosporangium* has *Roestelia*-type aecia and multiseptate teliospores without apparent spines or long projections, which clearly differs from the genus *Allodus* (Minnis et al. 2012). Besides, *Gymnosporangium* has Group V (type 4) spermogonia, *Roestelia*-type aecia and pedicellate teliospores, and these morphologies clearly differentiate it from *Neophysopella* in *Phakopsoraceae* s.lat., which has Group VI (type 7) spermogonia and sessile teliospores with 2–7 layers (Ji et al. 2019). In addition, *Gymnosporangium* differs from the genera *Austropuccinia*, *Dasyscypha*, *Puccorchidium*, *Sphaerophragmium* and *Sphenorchidium* in the family

Sphaerophragmiaceae, which has Group V (type 4) or Group VI (type 5) spermogonia, *Aecidium*-type aecia and teliospores with both vertically or transverse septa (Beenken 2017). Lastly, *Gymnosporangium* has a special host combination, with its telial stage occurring on gymnosperms and aecial stage on angiosperms. Such host alternation is distinctive from most of the rusts on gymnosperms, which have aecial stages on gymnosperms but uredinial/telial stages on angiosperms. Thus, we propose a new family, *Gymnosporangiaceae*, to accommodate the genus *Gymnosporangium* based on morphological differences and a molecular distinction from other families in the order *Pucciniales*.

Within the genus *Gymnosporangium*, sequence data were successfully generated from 184 specimens. Additional rDNA SSU, ITS and LSU sequences from 212 specimens from GenBank were aligned for phylogenetic analyses. In total a 2723 bp alignment of SSU, ITS and LSU, TrNef+G was selected as the best-fit substitution model. Maximum likelihood and Bayesian

analyses of the combined dataset resulted in similar topologies with only minor changes in poorly supported branches. Maximum likelihood best tree topology is shown in Fig. 2. These 396 specimens clustered into 32 well-supported phylogenetic groups. Among them, rust specimens on *Malus* were found in 22 phylogenetic groups. The morphological distinction in aecial or telial stages of these 22 groups were further characterised after examination by LM and SEM. With the aid of morphological and molecular data, a total of 22 *Gymnosporangium* species were confirmed occurring on *Malus* species. The connection of spermogonial/aecial and uredinial/telial stages of 13 species were further clarified. Species boundaries, host ranges and geographical distributions of all *Gymnosporangium* on *Malus* species were confirmed and illustrated below.

TAXONOMY

Family: Gymnosporangiaceae P. Zhao & L. Cai, *fam. nov.* — MycoBank MB831269

Etymology. Name derived from the type genus, *Gymnosporangium*.

Type genus. *Gymnosporangium* R. Hedw. ex DC., Fl. Franç. 2: 216. 1805.

Spermogonia Group V (type 4), bounding structures with well-developed peripheral flexuous hyphae. *Aecia* *Roestelia*-type, subepidermal, with well-developed peridia, aeciospores catenulate, with intercalary cells. *Uredinia* *Uredo*-type, subepidermal, urediniospores borne singly on pedicels. *Telia* subepidermal, erumpent as cushions, crests or horns, teliospores aseptate to multiseptate, borne singly on gelatinising pedicels. *Basidia* external.

Type species. *Gymnosporangium fuscum* DC., Fl. Franç. 2: 216. 1805, on *Juniperus sabina*.

GYMNOSPORANGIUM SPECIES ON MALUS

Gymnosporangium asiaticum Miyabe ex G. Yamada, Shokubutsu Byorigaku (Pl. Path) Tokyo Hakubunkwan 37(9): 304. 1904 — Fig. 3

Synonyms. *Roestelia koreensis* Henn. (as '*koreaënsis*'), Monsunia 1: 5. 1899.

Gymnosporangium photiniae F. Kern, Bull. New York Bot. Gard. 7: 443. 1911.

Gymnosporangium chinense Long, J. Agric. Res. 1(4): 354. 1914.

Gymnosporangium haraeenum Syd. & P. Syd., Ann. Mycol. 10(4): 405. 1912.

Gymnosporangium koreense H.S. Jacks., J. Agric. Res. 5: 1006. 1916.

Gymnosporangium spiniferum Syd. & P. Syd., Ann. Mycol. 10(1): 78. 1912.

Gymnosporangium taianum F. Kern, Mem. New York Bot. Gard. 10(5): 307. 1964.

Gymnosporangium unicorne H.Y. Yun, Mycologia 101(6): 806. 2009.

Typus. JAPAN, Hokkaido, Sapporo-shi, 0, I on *Cydonia vulgaris*, III on *J. chinensis*, K. Miyabe (lectotype designated here, MBT389888, Yamada (1904: 303 (0, I, III), f. 37).

Epitypification. JAPAN, Gifu prefecture, Mino, Kawaue-mura, III on *J. chinensis*, 3 Oct. 1912, K. Hara, CUP-0016 (epitype designated here, MBT389889), SSU, ITS and LSU sequences GenBank MN642598, MN642593 and MN642617.

Spermogonia not found. *Aecia* foliicolous and caulicolous, hypophyllous, roestelioid; peridium tubular, lacerating at apex or spreading, 4–7 mm high, peridial cells linear-rhomboid, 55–103 × 18–31 µm, outer walls smooth, inner walls small papillae and side walls moderately rugose; aeciospores globoid, ovoid, large coronate, 18–26 × 14–22 µm, walls yellowish, 1.0–2.0 µm thick. *Uredinia* absent. *Telia* foliicolous or on green stems, developing on witches' broom but without causing swelling on

stem, aggregated bluntly conical, hemispherical, pulvinate or somewhat wedge-shaped; 2–6 mm high, brownish orange; teliospores 2-celled, broadly to narrowly ellipsoid, 31–50 × 16–27 µm, walls 1.0–2.5 µm, pale orange to orange, pores 1 or 2 near septum or 1 apical in upper cell; pedicels cylindrical, hyaline, 2.5–5.0 µm diam.

Additional materials examined. CHINA, Beijing, Huai Rou District, 0, I on *M. pumila*, 2 May 2016, P. Zhao, ZP-R201, ZP-R203 & ZP-R204; Beijing, Yun Meng Mountain, 0, I on *M. pumila*, 11 July 2016, P. Zhao, ZP-R205, ZP-R215 & ZP-R228; Beijing, 0, I on *M. prunifolia*, Z.Y. Zhang, HMAS135598; Beijing, 0, I on *M. pumila*, 2 Aug. 1976, L. Guo, HMAS38650; Beijing, 0, I on *M. pumila*, 22 Oct. 1984, Y.C. Dai, HMAS56909; Beijing, 0, I on *M. spectabilis*, 2 Dec. 1947, F.L. Tai, HMAS12970; Beijing, Xiangshan Mountain, III on *J. chinensis*, 27 May 2006, L. Guo, HMAS172366; Beijing, Xiangshan Mountain, III on *J. chinensis*, 4 May 1979, Y.C. Wang, HMAS47229; Beijing, III on *J. chinensis*, 22 Mar. 1932, F.L. Tai, HMAS11935; Beijing, III on *J. chinensis*, 6 Apr. 1935, Y.C. Wang, HMAS22173; Guangdong, Guangzhou, III on *J. chinensis*, 26 Mar. 1973, Y.C. Wang, HMAS47228; Guang Xi, Shenmu, 27 Aug. 2015, P. Zhao, ZP-R876; Hebei, Qingyuan, 0, I on *Malus* sp., 18 Aug. 1932, Q.X. Wu, HMAS14327; Hei Longjiang, Greater Khingan Mountains, 10 Aug. 2015, P. Zhao, ZP-R960 & ZP-R961; Jiangsu, Nanjing, 0, I on *M. pumila*, 22 Sept. 1927, F.L. Tai, HMAS11217; Shaanxi, Wugong, 27 Aug. 1973, T.Y. Zhang, HMAS38649; Shaanxi, Xian, 0, I on *Pyrus bretschneideri*, 5 June 1939, collector unknown, HMAS33358; Sichuan, Chengdu, 18 May 1958, W.Q. Deng, HMAS26414; Sichuan, Yi Bin, 0, I on *M. pumila*, 18 May 2016, P. Zhao, ZP-R301; Tibet, Changdu, III on *J. tibetica*, 9 June 1976, Y.C. Chen, HMAS37835; Xinjiang, Altay, 0, I on *Malus* sp., 1 Sept. 1987, Z.Y. Zhao, HMAS92418 & HMAS92422; Yunnan, III on *J. chinensis*, 15 Apr. 1990, X.T. Zhou, HMAS165302; Yunnan, Kunming, 0, I on *M. pumila*, 13 May 2016, P. Zhao, ZP-R773, ZP-R774, ZP-R778 & ZP-R779; Yunnan, Kunming, III on *Cupressus duclouxiana*, 6 Apr. 1989, Y.X. Wang, HMAS135599. — USA, California, Berkeley, III on *J. excelsa*, 3 Sept. 1958, H.E. Parks, HMAS45640; New York, Ulster, 0, I on *Malus* sp., 28 Oct. 2009, H.E. Thomas, CUP-17524; Yonkers, 0, I on *M. ioensis* var. *plena*, 2 Aug. 1928, D.S. Welch, CUP-57311. — UK, III on *J. sabina*, 1 May 1889, C.B. Plowright, HMAS2503.

Host range and geographical distribution confirmed in this study — *Cupressus duclouxiana* — China; *Juniperus chinensis* cv. *globosa* — South Korea; *Juniperus chinensis* cv. *kaizuka* — South Korea; *Juniperus chinensis* cv. *sargentii* — South Korea; *Juniperus chinensis* — China, South Korea; *Juniperus sabina* — Japan, UK; *Juniperus tibetica* — China; *Malus asiatica* — China; *Malus ioensis* var. *plena* — USA; *Malus pumila* — China, Japan, USA; *Malus prunifolia* — China; *Malus spectabilis* — China; *Pyrus lindleyi* — China; *Pyrus pyrifolia* — China.

Additional host range and geographical distribution reported in previous studies — *Chaenomeles cardinalis* — Japan; *Chaenomeles cathayensis* — China; *Chaenomeles eburnea* — Japan; *Chaenomeles japonica* — Japan, South Korea; *Chaenomeles lagenaria* — Japan, South Korea; *Chaenomeles sinensis* — China, Japan, South Korea; *Chaenomeles speciosa* — China, Japan, South Korea; *Chaenomeles* × *superba* — Japan; *Crataegus cuneata* — China; *Crataegus pinnatifida* — China; *Crataegus wilsonii* — China; *Cydonia oblonga* — China; *Juniperus chinensis* var. *procumbens* — Japan; *Juniperus scopulorum* — Japan; *Juniperus scopulorum* var. *pyramidalis* — Japan; *Juniperus squamata* — Japan; *Juniperus virginiana* — Japan; *Photinia villosa* var. *brunnea* — South Korea; *Pyrus betulaeifolia* — China; *Pyrus bretschneideri* — China, Japan; *Pyrus calleryana* — China; *Pyrus communis* — China; *Pyrus montana* var. *rehderi* — China; *Pyrus pyrifolia* — Japan, South Korea, USA; *Pyrus serotina* — China; *Pyrus serrulata* — China; *Pyrus ussuriensis* — China, Japan, South Korea (Farr & Rossman 2019).

Notes — *Gymnosporangium asiaticum* was first reported on leaves of *J. chinensis* in Japan by Miyabe (1903), but he did not publish a description of this species in any form. Thereafter, Yamada (1904) validly described this species in the textbook of plant pathology with both description and line drawings. However, despite the existence of the valid name of *G. asiaticum*, Sydow & Sydow (1912) renamed rusts collected by K. Hara from at Kawaue-mura, Gifu prefecture of Japan as *G. haraeenum*. Subsequently, *G. haraeenum* was widely accepted as synonym of *G. asiaticum* due to its morphological similarities, host ranges and locality (Hiratsuka 1955, Hiratsuka et al. 1992). In addition, by using fresh materials from juniper from which Sydow's type was collected, Hara and other taxonomists confirmed leaf-inhabiting rusts on *J. chinensis* as *G. asiaticum* based on inoculation tests (Tanaka 1922). Due



Fig. 3 Morphology of *G. asiaticum*. a. Aecia (A) on the hypophyllous leaf surface; b. roestelioid aecia with peridia (P); c. ultrastructure of peridium observed by SEM; d. linear-rhomboid peridial cells observed by LM; e. ultrastructure of peridial cells observed by SEM, Out layer with smooth surface, inner surface with irregular papillae; f. globoid or ellipsoid aeciospores with verrucose spines; g. aeciospores with scattered germ pores (G); h. label of type specimen designated in this study; i. telia on the branches of *Juniperus* species; j. telia on green stems developing on witches' broom; k. 2-celled and pedicellate teliospores; l. teliospores with cylindrical, hyaline pedicels and germ pore (G). — Scale bars: c–g = 20 μ m; k–l = 20 μ m.

to the lack of holotype specimen information in the original description, and our failure to locate any type, we have designated illustrations of Yamada (1904) as lectotype. In addition, we designated an epitype specimen, which was collected by Hara in 1912 at Kawau-mura, Gifu prefecture of Japan. We successfully generated both morphological and molecular data from the epitype material. This species is hitherto reported from Asian countries, the East part of Russia and some regions in North America (Ziller 1974, Hiratsuka et al. 1992, Zhuang et al. 2012). It is still absent from the European Union and listed as a quarantine pest in the European and Mediterranean Plant Protection Organization (EPPO) A2 List due to its severe threat to apple and pear plantations (EPPO 2018). Hitherto, five *Gymnosporangium* species, *G. chinense*, *G. haraeumum*, *G. japonicum*, *G. koreense* and *G. spiniferum* were frequently regarded as synonyms of *G. asiaticum* (Kern 1973, Hiratsuka et al. 1992). Among them, these species with the exception of *G. japonicum*, were confirmed to be conspecific with *G. asiaticum* after systematic studies of type materials (Yun et al. 2009). Here we confirmed the species boundaries of *G. asiaticum*, and further revealed a recently proposed new species, *G. unicornis*, to be conspecific to *G. asiaticum*. In addition, *G. taianum* on *Cupressus duclouxiana* (HMAS135599), which has aecial hosts on *Chaenomeles*, *Crataegus*, *Photina* and telial hosts on *Juniperus* species and their varieties, is conspecific to *G. asiaticum*. According to Kern (1973), *G. asiaticum* has its telial stage on *Juniperus*, and has its aecial host on *Chaenomeles*, *Cydonia* and *Pyrus*. In this study, we reported five *Malus* species, i.e., *M. asiatica*, *M. ioensis* var. *plena*, *M. pumila*, *M. prunifolia* and *M. spectabilis*, as new aecial hosts. We also confirmed its telial hosts on *Cupressus duclouxiana*, *J. chinensis*, *J. sabina*, *J. tibetica* and their varieties.

***Gymnosporangium clavariiforme* (Wulfen) DC., Fl. Franç. 2: 217. 1805 — Fig. 4**

Basionym. *Tremella clavariiformis* Wulfen, (as '*clavariaeformis*'), *Collectanea ad botanicam, chemiam, et historiam naturalem spectantia* 2: 174. 1791.

Spermogonia not found. *Aecia* foliicolous and caulicolous, hypophyllous; peridium roestelioid, tubular, lacerating at apex or spreading, 1.5–3 mm high, peridial cells rhomboid, 77–148 × 15–29 µm, outer walls smooth, inner walls evenly echinulate; aeciospores globose, large coronate, 16–30 × 18–25 µm, walls yellowish, 1.0–3.0 µm thick. *Uredinia* absent. *Telia* caulicolous, aggregated, bluntly conical, hemispherical, pulvinate or somewhat wedge-shaped; 2–4 mm high, brownish orange; teliospores 2-celled, broadly to narrowly ellipsoid, 46–97 × 15–21 µm, walls 1.0–2.5 µm, pale orange to orange, pores 1 or 2 near septum or 1 apical in upper cell; pedicels cylindrical, hyaline, 3.0–7.5 µm diam.

Additional materials examined. GERMANY, Bavaria, Eichstätt, slope called Haselberg, c. 1 km NW of the municipal district Landershofen, limestone grassland with shrubs, on branches and twigs of *J. communis*, 14 Apr. 1991, *D. Triebel* & *G. Rambold*, *Microfungi Exsiccati* 90, HMAS67951. — USA, North Carolina, 0, I on *M. domestica*, 15 Sept. 1901, *A. George*, CUP-12076; Utah, Zion National Park, Kolob Canyon, 0, I on *Amelanchier* sp., 20 Aug. 1973, *collector unknown*, NYBG3011548; Wyoming, Laramie Mountains, III on *J. communis* var. *sibirica*, *G.B. Cummins*, NYBG3011553.

Host range and geographical distribution confirmed in this study — *Amelanchier* sp. — USA; *Juniperus communis* — Germany; *Juniperus communis* var. *sibirica* — USA; *Malus domestica* — USA.

Additional host range and geographical distribution reported in previous studies — *Amelanchier alnifolia* — Canada, USA; *Amelanchier bartramiana* — Canada, USA; *Amelanchier canadensis* — Canada, USA; *Amelanchier florida* — Canada, USA; *Amelanchier gaspensis* — Canada, USA; *Amelanchier humilis* — Canada, USA; *Amelanchier intermedia* — Canada, USA; *Amelanchier laevis* — Canada, USA; *Amelanchier lucida* — Canada; *Amelanchier oblongifolia* — USA; *Amelanchier ovalis* — Germany; *Amelanchier polycarpa*

— USA; *Amelanchier pumila* — USA; *Amelanchier rotundifolia* — Turkey; *Amelanchier spicata* — Canada, USA; *Amelanchier stolonifera* — USA; *Amelanchier utahensis* — USA; *Amelanchier wiegandii* — Canada, USA; *Aronia arbutifolia* — USA; *Cotoneaster integerrimus* var. *uniflorus* — Russia; *Cotoneaster melanocarpus* — Russia; *Cotoneaster nummularius* — Turkey; *Cotoneaster uniflorus* — Russia; *Crataegomespilus asnierei* — Sweden; *Crataegomespilus grandiflora* — Germany; *Crataegus aronia* — Turkey; *Crataegus azarolus* — Israel, Turkey; *Crataegus brevispina* — Spain; *Crataegus calycina* — Finland, Norway, Sweden; *Crataegus chrysocarpa* — Canada; *Crataegus columbiana* — Oregon; *Crataegus cuneata* — China; *Crataegus curvisepala* — Canada; *Crataegus dahurica* — Russia; *Crataegus heldreichii* — Greece; *Crataegus intricata* — Norway; *Crataegus laevigata* — Poland, UK; *Crataegus macracantha* — Norway; *Crataegus maximowiczii* — China, Russia; *Crataegus microphylla* — Turkey; *Crataegus monogyna* — Algeria, Bulgaria, Denmark, Finland, France, Germany, Greece, Iraq, Israel, Morocco, New Zealand, Norway, Poland, Spain, Sweden, UK, USSR; *Crataegus monogyna* subsp. *azarella* — Greece; *Crataegus monogyna* subsp. *monogyna* — Turkey; *Crataegus nigra* — Denmark, Norway, Sweden, USSR; *Crataegus orientalis* — Turkey; *Crataegus oxyacantha* — Canada, Denmark, Finland, France, Germany, Italy, Norway, Spain, Sweden, UK; *Crataegus oxyacantha* var. *rosea* — Canada; *Crataegus pentagyna* — Germany, Greece; *Crataegus pinnatifida* — China, South Korea; *Crataegus pinnatifida* var. *psiloda* — South Korea; *Crataegus rhipidophylla* — Canada; *Crataegus rhipidophylla* var. *rhipidophylla* — Poland; *Crataegus sanguinea* — Finland, Norway; *Crataegus scabrifolia* — China; *Crataegus sorbifolia* — Germany; *Crataegus succulenta* — Canada, Norway; *Crataegus wilsonii* — China; *Crataegus* × *lambertiana* — Norway; *Cydonia oblonga* — Canada, Greece, USA; *Cydonia vulgaris* — Canada, USA; *Juniperus communis* — Austria, Denmark, Finland, France, Germany, Greece, New Zealand, Norway, Poland, Spain, Sweden, UK, USA; *Juniperus communis* var. *depressa* — Canada, USA; *Juniperus communis* var. *hibernica* — USA; *Juniperus communis* var. *stricta* — Denmark; *Juniperus drupacea* — Turkey; *Juniperus excelsa* — Turkey; *Juniperus foetidissima* — Turkey; *Juniperus nana* — Russia; *Juniperus oxycedrus* — Bulgaria, France, Germany, Greece, Spain, Turkey, USSR; *Juniperus rigida* — Korea; *Juniperus sibirica* — Russia; *Malus sylvestris* — Greece, Turkey; *Mespilus germanica* — Turkey; *Pyrus arbutifolia* — USA; *Pyrus communis* — Canada, Denmark, Greece, Iraq, Norway, Poland, Sweden, UK, USA; *Pyrus pyrifolia* — USA; *Pyrus syriaca* — Turkey; *Pyrus* × *communis* — Norway; *Sorbus aria* — Greece, Norway; *Sorbus aucuparia* — Bulgaria; *Sorbus intermedia* — Norway; *Sorbus prattii* — China (Farr & Rossman 2019).

Notes — *Gymnosporangium clavariiforme* was initially described on *J. communis*, and is characterised by its large peridial cells with sparsely echinulate papillae and caulicolous telia with narrowly ellipsoid teliospores (Kern 1908, 1911, Yun et al. 2009). The aecial stage was confirmed on the plant genera *Amelanchier*, *Aronia*, *Cotoneaster*, *Crataegus*, *Cydonia*, *Malus*, *Pyrus* and *Sorbus* (Kern 1973, Farr & Rossman 2019). This species is relatively common in temperate regions in Asia, Europe and North America (Tai 1979, Wang & Guo 1985, Yun et al. 2009, Zhuang et al. 2012). Based on morphological and molecular data, *M. domestica* was further confirmed as one new aecial host.

***Gymnosporangium clavipes* Cooke & Peck, Ann. Rep. N.Y. State Mus. Nat. 25: 89. 1873 — Fig. 5**

Synonyms. *Caeoma germinale* Schwein., *Trans. Amer. Philos. Soc.* 4(2): 294. 1832.

Gymnosporangium germinale F. Kern, *Bull. Torrey Bot. Club* 35: 506. 1908.

Podisoma clavipes Cooke & Peck, *J. Quekett Micros. Club* 2: 267. 1871.

Typus. USA, New York, Albany, Bethlehem, III on *J. virginiana*, *P.H. Charles*, NYS-F-775 (isotype), SSU, ITS and LSU sequences GenBank MK488179, MK518847 and MK518583.

Spermogonia not found. *Aecia* mainly fructicolous, sometimes caulicolous, roestelioid; peridium cylindrical, becoming fimbriate, 0.5–2 mm high, peridial cells rhomboid, 69–105 × 33–51 µm, outer walls smooth, inner walls tuberculate, verrucose with ridge-like papillae; aeciospores globose, echinulate, 27–49 × 24–37 µm, walls yellowish, 2.0–5.0 µm thick. *Uredinia* absent. *Telia* caulicolous on fusiform swellings of the smaller branches, applanate, dark brown, becoming tremelloid or patelliform when

expanded, frequently covering the whole hypertrophied area; teliospores 2-celled, ellipsoid, $32\text{--}85 \times 23\text{--}32 \mu\text{m}$, walls $1.0\text{--}2.5 \mu\text{m}$, pale orange to orange, pores 1 or 2 near septum or 3 apical in upper cell, pedicels carotiform, $10\text{--}24 \mu\text{m}$ diam near the pore.

Additional materials examined. CANADA, Quebec, 0, I on *Malus* sp., 13 Aug. 1957, J.A. Parmelee, CUP-48508. – USA, New York, 0, I on *Malus* sp., date and collector unknown, CUP-13530; Massachusetts, III on *J. virginiana*, 5 May 1966, collector unknown, NYBG3011007; Missouri, 0, I on *Crataegus* sp., 12 July 1990, J. Ewan, NYBG461394; New York, Tompkins, Ithaca, Woods, III on *J. virginiana*, 28 May 1904, W.D. Benjamin, CUP-18207.

Host range and geographical distribution confirmed in this study — *Crataegus* sp. – USA; *Juniperus virginiana* – USA; *Malus domestica* – USA; *Malus* sp. – Canada, USA; *Pyrus calleryana* – USA.

Additional host range and geographical distribution reported in previous studies — *Amelanchier alnifolia* – Canada, USA; *Amelanchier alnifolia* var. *semiintegrifolia* – Canada; *Amelanchier arborea* – USA; *Amelanchier bartramiana* – Canada, USA; *Amelanchier canadensis* – Canada, USA; *Amelanchier florida* – Canada; *Amelanchier humilis* – Canada, USA; *Amelanchier huronensis* – Canada; *Amelanchier intermedia* – Canada, USA; *Amelanchier laevis* – Canada; *Amelanchier lucida* – Canada; *Amelanchier oblongifolia* – USA; *Amelanchier sanguinea* – Canada, USA; *Amelanchier spicata* – Canada, USA; *Aronia arbutifolia* – Canada, USA; *Aronia floribunda* – Canada, USA; *Aronia melanocarpa* – Canada, USA; *Aronia prunifolia* – USA; *Chaenomeles japonica* – USA; *Cotoneaster acutifolia* – Canada, USA; *Cotoneaster acutifolius* – Canada; *Cotoneaster lucida* – Canada; *Crataegus aestivalis* – USA; *Crataegus beata* – Canada; *Crataegus caesia* – Canada; *Crataegus chrysoarpa* – Canada; *Crataegus coccinea* – USA; *Crataegus columbiana* – Canada; *Crataegus crus-galli* – USA; *Crataegus curvisepala* – Canada; *Crataegus douglasii* – Canada, USA; *Crataegus fucosa* – Canada,



Fig. 4 Morphology of *G. clavariiforme*. a. Aecia (A) on the hypophyllous leaf surface; b. aecia on fruit; c. ultrastructure of peridia (P) observed by SEM; d. rhomboid peridial cells observed by LM; e. ultrastructure of peridial cells observed by SEM; f. globose or ellipsoid aeciospores with scattered germ pores (G) observed by LM; g. verrucose aeciospores observed by SEM; h. telia on the branches of *Juniperus* species; i. label of type specimen designated in this study; j. telia (T) on branches of *Juniperus* species; k. 2-celled and pedicellate teliospores; l. teliospores with cylindrical and hyaline pedicels. — Scale bars: c = 200 μm ; d–e = 50 μm ; f–g, k–l = 20 μm .

USA; *Crataegus mexicana* – Mexico; *Crataegus michauxii* – USA; *Crataegus monogyna* – Canada; *Crataegus oxyacantha* – Canada, USA; *Crataegus pedicellata* – Canada, USA; *Crataegus punctata* – Canada, USA; *Crataegus spathulata* – USA; *Crataegus succulenta* – Canada; *Cydonia oblonga* – Canada, USA; *Cydonia vulgaris* – USA; *Juniperus chinensis* – Canada, USA; *Juniperus communis* – Canada, USA; *Juniperus communis* var. *depressa* – Canada, USA; *Juniperus horizontalis* – Canada, USA; *Juniperus phoenicea* – Portugal; *Juniperus scopulorum* – Canada, USA; *Juniperus virginiana* var. *depressa* – Canada; *Mespilus germanica* – USA; *Photinia villosa* – USA; *Pyrus arbutifolia* – Canada; *Pyrus communis* – USA; *Pyrus pyrifolia* – USA; *Sorbus americana* – Canada, USA; *Sorbus aucuparia* – Canada; *Sorbus decora* – Canada; *Sorbus occidentalis* – Canada; *Sorbus sitchensis* – Canada; *Sorbus sitchensis* var. *grayii* – Canada; *Sorbus sitchensis* var. *sitchensis* – Canada (Farr & Rossman 2019).

Notes — *Gymnosporangium clavipes* was one of earliest species reported from North America, and is characterised by its relatively large aeciospores with tuberculate peridial cells, 2-celled teliospores with carotiform pedicels. The aecial stage of this species was first described as *Caeoma germinale* on *Crataegus* species, and the telial stage was described on *J. virginiana* as '*Podisoma clavipes*' (Arthur 1934). Later these two species were confirmed as two phases of *G. clavipes*, and host ranges of this species was systematically reported based

on inoculation tests (Crowell 1940). Host alternation of this species was reported on *Juniperus* and a series of species in *Amelanchier*, *Aronia*, *Chaenomeles*, *Crataegus*, *Cydonia*, *Malus*, *Mespilus* and *Photinia* in the *Rosaceae* (Crowell 1940, Laundon 1977). In the aecial stage, several *Malus* species, i.e., *M. angustifolia*, *M. floribunda*, *M. pumila*, *M. spectabilis*, *M. sylvestris* and several unidentified *Malus* species were reported as aecial hosts of *G. clavipes* (Farr & Rossman 2019). *Gymnosporangium clavipes* is distributed in North America, Central America and Caribbean countries, and it is listed as one of the important quarantine pests in the EU and Asian countries (EPPO 2018). Here we successfully generated sequence data from the type material, and further confirmed host alternation of *G. clavipes* on *J. virginiana* and species of *Crataegus*, *Malus*, *Pyrus* and related species.

Gymnosporangium corniculans F. Kern, Mycologia 2(5): 236. 1910

Spermogonia not found. *Aecia* foliicolous or caulicolous, hypophyllous, roestelioid; peridium cornute, tardily dehiscent by side lacerations, 1.5–3.5 mm high, causing hypertrophy, peridial

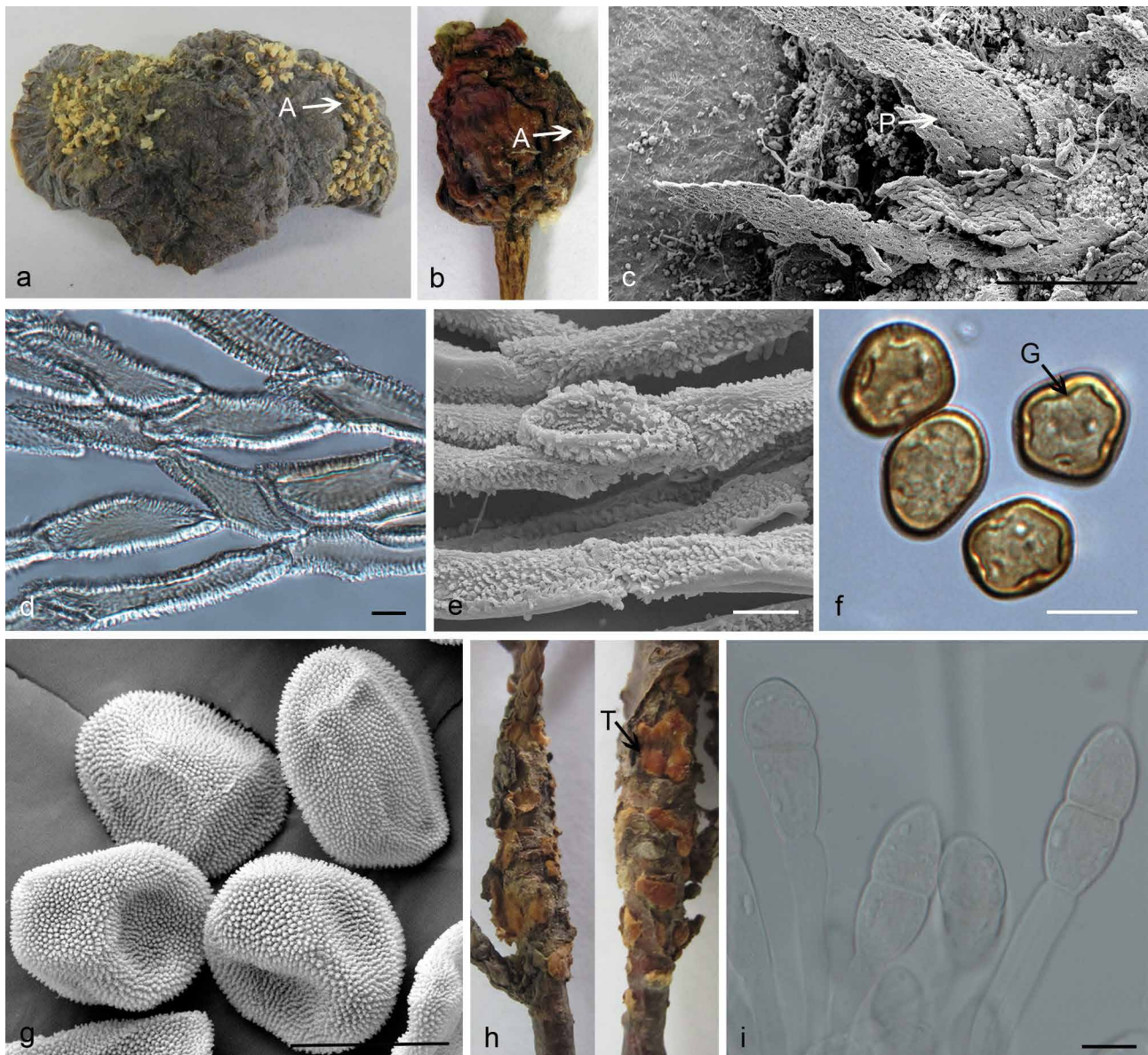


Fig. 5 Morphology of *G. clavipes*. a. Aecia (A) on the surface of fruits; b. aecia on the fruits; c. ultrastructure of peridia (P) observed by SEM; d. rhomboid peridial cells observed by LM; e. ultrastructure of peridial cells observed by SEM; f. globoid or ellipsoid aeciospores with scattered germ pores (G) observed by LM; g. verrucose aeciospores observed by SEM; h. telia (T) on the branches of *Juniperus* species; i. 2-celled teliospores with pedicels carotiform, with up to 24 µm near the pore. — Scale bars: c = 200 µm; d–g, i = 20 µm.

cells rhomboid, 55–103 × 18–31 µm, outer walls smooth, side walls rugose, inner walls with small papillae of irregular shape, densely distributed; aeciospores globoid, ovoid, large coronate, 18–34 × 16–27 µm, walls yellowish, 1.0–2.5 µm thick. *Uredinia* absent. *Telia* caulicolous, globoid galls generally 3–12 mm diam, terete, cylindrical to acuminate, brownish orange; teliospores 2-celled, broadly to narrowly ellipsoid, 31–56 × 16–30 µm, walls 1.0–2.5 µm, pale orange to orange, pores 1 or 2 near septum; pedicel cylindrical, hyaline, 2.0–3.5 µm diam.

Materials examined. CHINA, Guizhou, Anshun, III on *J. chinensis*, 1 Apr. 1999, M.H. Liu, HMAS79065. – USA, Connecticut, East Grandy, 0, I on *M. domestica*, 29 Aug. 1931, Spaulding & Eno, CUP-19705 & CUP-19706; New York, Tompkins, Ithaca, 0, I on *A. canadensis*, date unknown, H.H. Whetzel, CUP-3087.

Host range and geographical distribution confirmed in this study — *Amelanchier canadensis* – USA; *Juniperus chinensis* – China; *Juniperus horizontalis* – USA; *Malus domestica* – USA.

Additional host range and geographical distribution reported in previous studies — *Amelanchier alnifolia* – Canada; *Amelanchier intermedia* – USA; *Amelanchier oblongifolia* – USA; *Amelanchier rotundifolia* – USA; *Amelanchier sanguinea* – Canada, USA; *Juniperus virginiana* – USA (Farr & Rossman 2019).

Notes — This species is characterised by its cornuted form of the aecia and small papillae of irregular shape in peridial cells. It was first described on *J. horizontalis* in Michigan in the USA and Canada (Kern 1964). This species is mainly reported with their aecial stage on *Amelanchier* in North America. In this study we found *M. domestica* as a new aecial host. We further confirmed it occurs in China, the first record outside North America.

Gymnosporangium cornutum Arthur ex F. Kern, Bull. New York Bot. Gard. 7: 444. 1911

Spermogonia not found. *Aecia* foliicolous and caulicolous, hypophyllous; peridium tubular, lacerating at apex or spreading, 4–7 mm high, peridial cells rhomboid, 55–103 × 18–31 µm, outer walls smooth, inner walls small papillae with irregular shape and side walls moderately rugose; aeciospores globoid, ovoid, minute coronate, 18–26 × 14–22 µm, walls yellowish, 1.0–2.0 µm thick. *Uredinia* absent. *Telia* foliicolous or on green stems, developing on witches' broom but without causing swelling on stem, aggregated bluntly conical, hemispherical, pulvinate or somewhat wedge-shaped, 2–6 mm high, brownish orange; teliospores 2-celled, broadly to narrowly ellipsoid, 31–50 × 16–27 µm, walls 1.0–2.5 µm, pale orange to orange, pores 1 or 2 near septum or 1 apical in upper cell, pedicel cylindrical, hyaline, 2.0–4.5 µm diam.

Materials examined. AUSTRIA, Carinthia, Koralpe, 0, I on *S. aucuparia*, 28 Aug. 2011, C. Scheuer, NYBG463. – CHINA, Beijing, 0, I on *M. spectabilis*, 2 June 1947, HMAS12940. – FINLAND, Kiiminki, 0, I on *S. aucuparia*, 30 July 1962, P.S. Jokela, NYBG3011886. – USA, Connecticut, III on *J. virginiana*, 11 June 1964, C.T. Rogerson, NYBG3070932.

Host range and geographical distribution confirmed in this study — *Juniperus virginiana* – USA; *Malus spectabilis* – China; *Sorbus aucuparia* – Austria, Finland.

Additional host range and geographical distribution reported in previous studies — *Amelanchier ovalis* – Germany; *Juniperus communis* – Bulgaria, Denmark, Finland, Norway, Poland, Sweden, Turkey, UK, USA; *Juniperus communis* var. *depressa* – Canada, USA; *Juniperus communis* var. *montana* – Japan; *Juniperus communis* var. *nipponica* – Japan; *Juniperus conferta* – Japan; *Juniperus rigida* – China, Japan, South Korea; *Juniperus sibirica* – Japan, Russia, USA; *Malus fusca* – Canada; *Malus pumila* – Greece; *Malus sylvestris* – Greece; *Pyrus americana* – USA; *Pyrus aucuparia* – USA; *Pyrus sitchensis* – USA; *Sorbus alnifolia* – South Korea; *Sorbus americana* – Canada, Norway; *Sorbus amurensis* – Russia; *Sorbus aria* – Greece; *Sorbus arranensis* – Norway; *Sorbus aucuparia* – Belarus, Bulgaria, Canada, Denmark, Germany, Japan, Norway, Poland, Russia, Sweden, Turkey, UK; *Sorbus commixta* – Japan; *Sorbus decora* – Canada; *Sorbus discolor* – China;

Sorbus hybrida – Denmark, Finland, Norway, Sweden; *Sorbus intermedia* – Finland, Norway, Sweden; *Sorbus intermedia* var. *arranensis* – Norway; *Sorbus kamtschatcensis* – Russia; *Sorbus koehneana* – China; *Sorbus meinichii* – Finland, Norway; *Sorbus neglecta* – Norway; *Sorbus occidentalis* – Canada; *Sorbus sambucifolia* – Japan, Russia; *Sorbus sambucifolia* var. *pseudogracilis* – Japan; *Sorbus sargentiana* – UK; *Sorbus scopulina* – Canada; *Sorbus sibirica* – Russia; *Sorbus sitchensis* – Canada; *Sorbus sitchensis* var. *grayii* – Canada; *Sorbus sitchensis* var. *sitchensis* – Canada; *Sorbus tianschanica* – China, Norway; *Sorbus umbellata* – Turkey; *Sorbus ursina* – Nepal; *Sorbus × thuringiaca* – UK (Farr & Rossman 2019).

Notes — *Gymnosporangium cornutum* was first described on *J. sibirica* in Colorado in the USA, and it was recorded on three *Malus* species (i.e., *M. fusca*, *M. pumila* and *M. sylvestris*) in North America and Europe (Farr & Rossman 2019). Here we confirmed *M. spectabilis* as an additional aecial host for this species.

Gymnosporangium fenzelianum F.L. Tai & C.C. Cheo, Bull. Chin. Bot. Soc. 3: 60. 1937 — Fig. 6

Synonym. *Roestelia fenzeliana* (F.L. Tai & C.C. Cheo) F. Kern, Revised Taxonomic Account of *Gymnosporangium* (Univ. Park & London): 85. 1973.

Typus. CHINA, Shaanxi, Taibai Mountain, 0, I on *M. kansuensis*, 23 Aug. 1934, F.L. Tai, HMAS6983 (holotype).

Epitypification. CHINA, Shaanxi, Taibai Mountain, 0, I on *M. kansuensis*, 28 July 1938, Y.C. Wang, HMAS33357 (epitype designated here, MBT388922), ITS and LSU sequences GenBank MN605695 and MN605773.

Spermogonia, *uredinia* and *telia* not found. *Aecia* foliicolous, hypophyllous, roestelioid; peridium tubular, cornuted, spreading or erect after dehiscence, 0.8–1.5 mm high, peridial cells prismatic, 43–96 × 27–64 µm, rugose with closely set ridges of various length; aeciospores globoid, ovoid, verrucose, 22–36 × 20–24 µm, walls slightly brown, 1–3 µm thick, germ pores scattered, 4–8.

Additional materials examined. CHINA, Shaanxi, Taibai Mountains, 0, I on *M. kansuensis*, 26 June 1958, Y.C. Wang, HMAS24436; Shaanxi, Taibai Mountains, 0, I on *M. kansuensis*, 9 Sept. 1958, Y.C. Wang, HMAS24438; Shaanxi, Taibai Mountains, 0, I on *M. kansuensis*, 11 Aug. 2014, P. Zhao, ZP-R3 & ZP-R14; Gansu, Zhouqu, 3 Sept. 1992, J. Y. Zhuang, HMAS172210.

Host range and geographical distribution — *Malus kansuensis* – China.

Notes — *Gymnosporangium fenzelianum* was first reported on *M. kansuensis* in China (Tai 1979), and it is characterised by its lanceolate spindles on peridial cells and relatively large aeciospores. This species was once transferred to the genus *Roestelia*, and a new combination *R. fenzeliana* was proposed (Kern 1973). Here we resurrected the name *G. fenzelianum*, and introduced an epitype for this species. Although we failed to find the telial stage of this species, morphological and phylogenetic distinction of this species from other *Gymnosporangium* species was confirmed.

Gymnosporangium globosum (Farl.) Farl., Bot. Gaz. 11(9): 236. 1886

Basionym. *Gymnosporangium fuscum* var. *globosum* Farl., Anniv. Mem. Boston. Soc. Nat. Hist.: 34. 1880.

Spermogonia not found. *Aecia* hypophyllous, foliicolous and caulicolous, roestelioid; peridium cylindrical, becoming fimbriate 0.5–2 mm high, peridial cells rhomboid, 69–105 × 33–51 µm, outer walls smooth, side walls rugose, inner walls small papillae with irregular verruculose with ridge-like papillae; aeciospores globoid, large coronate, 27–49 × 24–37 µm, walls yellowish, 2.0–5.0 mm thick. *Uredinia* absent. *Telia* caulicolous on fusiform or gall-like swellings of the smaller branches, applanate, dark brown, becoming tremelloid or patelliform when expanded; teliospores 2-celled, ellipsoid, 32–85 × 23–32 µm, walls 1.0–2.5



Fig. 6 Morphology of *G. fenzelianum*. a. Labels of the holotype specimen; b. acelia (A) on the hypophyllous leaf surface; c. rhomboid or oblong peridial cells observed by LM; d. ultrastructure of peridial cells observed by SEM; e. globose or ellipsoid aeciospores with scattered germ pores observed by LM; f. verrucose aeciospores observed by SEM. — Scale bars: c–f = 20 μ m.

mm, pale orange to orange, pores 1 or 2 near septum or 3 apical in upper cell, pedicel cylindrical, hyaline, 2.5–3.0 μ m diam.

Additional materials examined. USA, Massachusetts, 0, 1 on *Crataegus* sp., 13 Sept. 1966, H.E. Bigelow, NYBG4897; New York, Bronx County, 0, 1 on *Crataegus* sp., 16 July 1978, collector unknown, NYBG3010437; New York, Bronx County, 111 on *Juniperus* sp., 21 May 1983, collector unknown, NYBG3010436; New York, Geneva, 0, 1 on *Malus* sp., 22 Aug. 1908, J.A. Maney, CUP-1553; New York, Tompkins County, 111 on *J. virginiana*, 10 May 1946, collector unknown, NYBG3010433.

Host range and geographical distribution confirmed in this study — *Crataegus* sp. — USA; *Juniperus virginiana* — USA; *Juniperus* sp. — USA; *Malus* sp. — USA.

Additional host range and geographical distribution reported in previous studies — *Amelanchier* \times *humilis-laevis* — USA; *Crataegus acutiloba* — USA; *Crataegus anomala* — Canada, USA; *Crataegus apposita* — USA; *Crataegus asperifolia* — USA; *Crataegus beata* — Canada; *Crataegus brainerdii* — USA; *Crataegus brunetiana* — Canada, USA; *Crataegus caesia* — Canada; *Crataegus calpodendron* — Canada, USA; *Crataegus chrysoarpa* — Canada; *Crataegus*

chrysoarpa var. *phoenicea* — Canada; *Crataegus coccinea* — Canada, USA; *Crataegus coccinioides* — USA; *Crataegus colorata* — USA; *Crataegus conjuncta* — USA; *Crataegus conspicua* — USA; *Crataegus crus-galli* — Canada, USA; *Crataegus curvisepala* — Canada; *Crataegus cyclophylla* — USA; *Crataegus delectabilis* — Canada; *Crataegus delucida* — USA; *Crataegus demissa* — USA; *Crataegus dissimilis* — USA; *Crataegus dissona* — USA; *Crataegus eamesi* — USA; *Crataegus edsoni* — USA; *Crataegus egglestonii* — USA; *Crataegus festiva* — USA; *Crataegus floribunda* — Canada, USA; *Crataegus forbesae* — USA; *Crataegus fetalis* — USA; *Crataegus fuscosa* — Canada, USA; *Crataegus genialis* — USA; *Crataegus glandulosa* — Canada, USA; *Crataegus glaucophylla* — Canada, USA; *Crataegus gracilior* — USA; *Crataegus holmesiana* — USA; *Crataegus intricata* — Canada, USA; *Crataegus jesupii* — USA; *Crataegus lavalleyi* — USA; *Crataegus macracantha* — Canada, USA; *Crataegus macrosperma* — USA; *Crataegus margareta* — Canada, USA; *Crataegus mcgeeae* — USA; *Crataegus membranacea* — USA; *Crataegus mexicana* — USA; *Crataegus mollis* — Canada, USA; *Crataegus monogyna* — Canada, USA; *Crataegus neo-londinensis* — USA; *Crataegus neofluviatilis* — USA; *Crataegus oxyacantha* — Canada, USA; *Crataegus pedicellata* — Canada; *Crataegus pedicillata* — Canada; *Crataegus pentandra* — USA; *Crataegus pequotorum* — USA; *Crataegus pertomentosa* — USA; *Crataegus*

pinnatifida – South Korea; *Crataegus pinnatifida* var. *major* – South Korea; *Crataegus pisifera* – USA; *Crataegus pringlei* – USA; *Crataegus pruinosa* – USA; *Crataegus pruinosa* var. *latisejala* – USA; *Crataegus punctata* – USA; *Crataegus quinebaugensis* – USA; *Crataegus rhombifolia* – USA; *Crataegus roanensis* – Canada, USA; *Crataegus rotundifolia* – Canada, USA; *Crataegus sanguinea* – Canada, USA; *Crataegus scabrida* – USA; *Crataegus schweinitziana* – USA; *Crataegus silvicola* var. *beckwithae* – USA; *Crataegus straminea* – USA; *Crataegus submollis* – Canada, USA; *Crataegus succulenta* – USA; *Crataegus tenella* – USA; *Crataegus tomentosa* – Canada, USA; *Crataegus viridis* – USA; *Juniperus barbadensis* – China; *Juniperus*

chinensis – Canada, USA; *Juniperus communis* var. *depressa* – USA; *Juniperus horizontalis* – Canada, China, USA; *Juniperus prostrata* – USA; *Juniperus scopulorum* – Canada; *Juniperus silicicola* – USA; *Juniperus virginiana* – USA; *Malus angustifolia* – USA; *Malus baccata* – USA; *Malus domestica* – USA; *Malus floribunda* – USA; *Malus pumila* – Canada; *Malus sylvestris* – USA; *Pyrus americana* – USA; *Pyrus angustifolia* – USA; *Pyrus communis* – Canada, USA (Farr & Rossman 2019).

Notes — This species was first reported on *J. virginiana* in the USA (Farlow 1906). It resembles *G. sabiniae* but differs

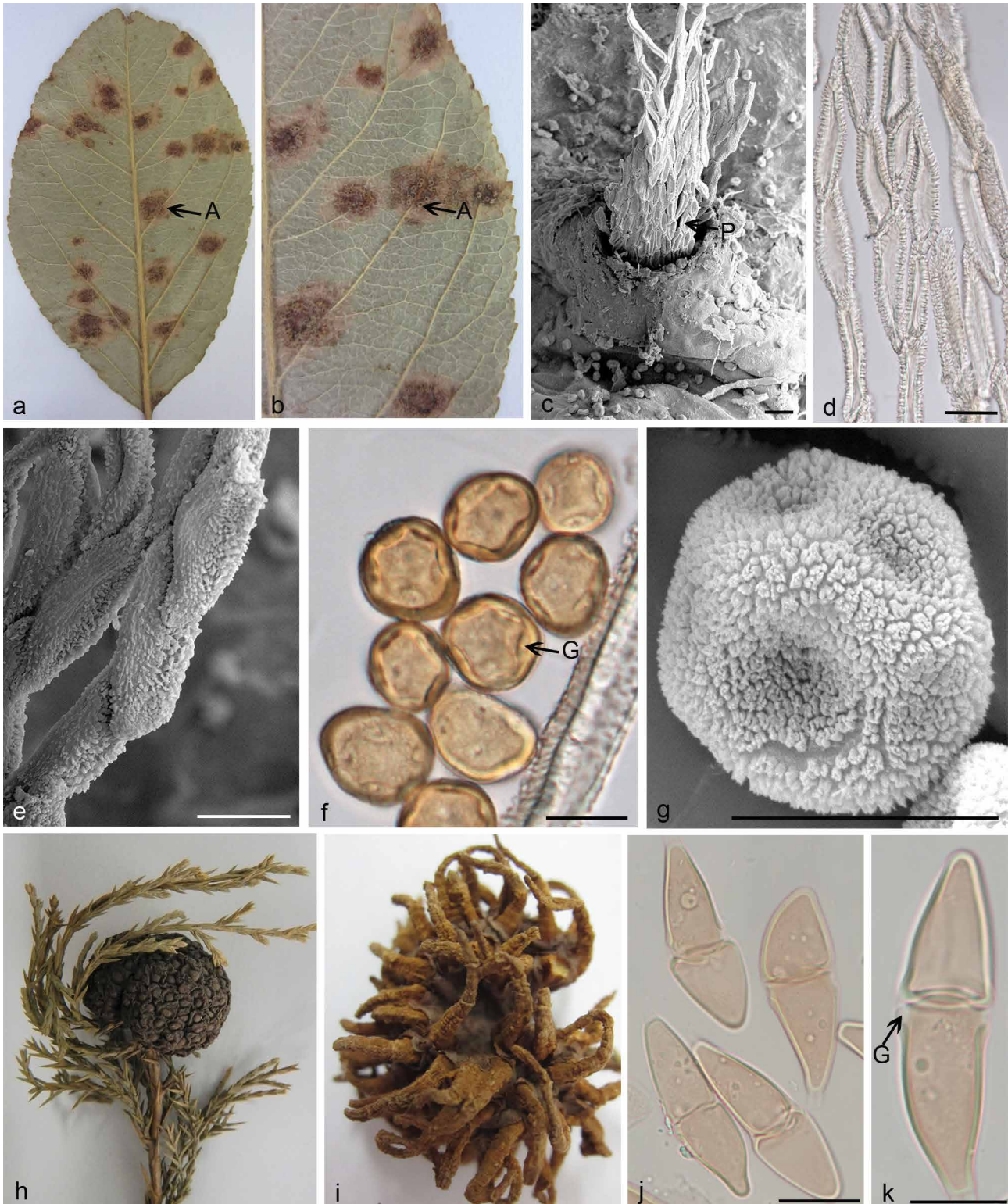


Fig. 7 Morphology of *G. juniperi-virginianae*. a. Aecia (A) on the hypophyllous leaf surface; b. foliicolous and roestelioid aecia (A) on the leaf surface; c. roestelioid aecia with tubular peridium (P) observed by SEM; d. rhomboid peridial cells observed by LM; e. ultrastructure of peridial cells observed by SEM; f. globose or ellipsoid aeciospores with scattered germ pores (G) observed by LM; g. verrucose aeciospores with large coronate papillae observed by SEM; h. cauliculous telia formed globose galls on stem of juniper. i. globose telia with cylindrical-acuminate sori; j. 2-celled and pedicellate teliospores with cylindrical and hyaline pedicels; k. teliospores with germ pores (G). — Scale bars: c–e = 50 µm; f–g, j–k = 20 µm.

in its telia with globose galls, roestelioid aecia and the ultra-structure of peridial cells and aeciospores. Five *Malus* species, i.e., *M. angustifolia*, *M. baccata*, *M. floribunda*, *M. pumila* and *M. sylvestris*, were reported as hosts of *G. globosum*, and this species was listed as an important quarantine pest in the EU and China (EPPO 2018) although existence of this species in China has already been reported (Zhuang et al. 2012). Here we confirmed the delimitation of this species, and further clarified the host alternation between *Crataegus*, *Juniperus* and *Malus*.

***Gymnosporangium juniperi-virginianae* Schwein., Schr. Nat. Ges. Leipzig 1: 74. 1822 — Fig. 7**

Synonyms. *Gymnosporangium macropus* Link, Willd. Sp. Pl. 4, 6(2): 128. 1825.

Gymnosporangium virginianum Spreng., Syst. Veg., edn. 16, 4(1): 562. 1827.

Podisoma juniperi-virginianae (Schwein.) Fr., Syst. Mycol. (Lundae) 3(2): 507. 1832.

Aecidium pyratum Schwein., Trans. Amer. Philos. Soc., n. s. 4(2): 2896. 1832.

Roestelia pyrata (Schwein.) Thaxt., Proc. Amer. Acad. Arts 22: 262. 1886.

Roestelia pyrata (Schwein.) Plowr., Monogr. Brit. Ured. Ustil. (London): 57. 1889.

Typus. USA, North Carolina, Carteret, on *J. virginiana*, 3 Apr. 1977, J.J. Kohlmeyer, NYBG1391099 (neotype designated here, MBT388923), SSU, ITS and LSU sequences GenBank MN604985, KU288647 and KU342712.

Spermogonia not found. *Aecia* foliicolous, hypophyllous, roestelioid; peridium tubular, at first cylindrical, fimbriate to base and strongly recurved, 0.5–1.5 mm high, peridial cells long and narrow, 67–103 × 16–43 µm, much curved, outer walls with smooth surface, inner walls with small papillae and walls moderately rugose; aeciospores globoid, ovoid or broadly ellipsoid, 18–34 × 14–22 µm, walls yellowish, 1.0–3.0 µm thick, walls surface with large coronate papillae. *Uredinia* absent. *Telia* cauliculous, on globoid or reniform galls, 10–40 mm diam, cylindrical or cylindrical-acuminate, golden-brown or somewhat reddish surrounded at base by a raised ring of host tissue, 1–4 cm long, orange; teliospores 2-celled, ellipsoid, 35–66 × 16–23 µm, walls 1.0–2.5 µm, brownish, pores 2, septate, pedicel cylindrical, hyaline, 2.5–3.5 µm diam.

Additional materials examined. USA, Connecticut, 0, I on *M. pumila*, 4 Sept. 1931, G.H. Hepting, CUP-19812; Columbia, Clermont, 0, I on *Malus* sp., 1 Aug. 1909, H. Wilson, CUP-28110; Connecticut, Cos Cob, Montgomery Nursery, III on *J. scopulorum*, 8 Mar. 1932, collector unknown, CUP-57206; Connecticut, III on *J. virginiana*, 11 May 1992, S.R. Hill, NYBG23036; Dakota, III on *J. scopulorum*, 11 June 1927, Brenckle & Stevens, HMAS2218; Indiana, Avilla, 0, I on *Malus* sp., 8 May, 1908, H.H. Whetzel, CUP-2985; Indiana, 0, I on *J. virginiana*, 11 May 1900, J.C. Arthur, HMAS43709; Indiana, 0, I on *M. coronaria*, 12 July 1902, H.H. Thomas, CUP-45235; Iowa, Ames, III on *Juniperus* sp., 1 Nov. 1929, D.B. Yu, HMAS14325; Iowa, III on *Juniperus* sp., N.L. Gardner, HMAS49243; Iowa, 0, I on *M. coronaria*, 31 July 1899, H.H. Thomas, CUP-55712; Massachusetts, III on *J. virginiana*, date unknown, H.E. Ahles, NYBG237046; Massachusetts, 0, I on *M. domestica*, 22 Aug. 1910, collector unknown, CUP-21697 & CUP-25670; Massachusetts, 0, I on *M. domestica*, 26 Sept. 1931, collector unknown, CUP-19919; New York, Dutchess, Hyde Park, III on *J. virginiana*, 14 May, 1968, H.E. Ahles, NYBG3011022 & NYBG3011024; New York, 0, I on *M. glaucescens*, 26 Sept. 1917, collector unknown, CUP-594; New York, 0, I on *M. ioensis*, 26 Sept. 1917, collector unknown, CUP-595; New York, 0, I on *M. domestica*, 15 June 1908, collector unknown, CUP-21686 & CUP-17321; New York, 0, I on *M. domestica*, 9 Sept. 1925, collector unknown, CUP-14980; New York, 0, I on *M. domestica*, 9 Sept. 1930, collector unknown, CUP-882, CUP-20156, CUP-20157, CUP-20160, CUP-20161, CUP-20162, CUP-20164, CUP-20165, CUP-20166, CUP-20202, CUP-20208, CUP-20209, CUP-20210 & CUP-20211; New York, 0, I on *M. soulardi*, 27 Sept. 1917, collector unknown, CUP-596; North Carolina, Carteret, on *J. virginiana*, 3 Apr. 1977, J.J. Kohlmeyer, NYBG461220; New York, III on *J. virginiana*, 4 June 1967, collector unknown, NYBG237070; North Carolina, 0, I on *M. coronaria*, 25 July 1934, G.B. Cummins, CUP-24473; North Dakota, III on *Juniperus* sp., 12 Aug. 1915, O.A. Stevens, HMAS6725; Tennessee, Cades Cove, Smoky Mountains Park, 0, I on *M. angustifolia*, G.B. Cummins, CUP-4826; Tennessee, 0, I on *M. angustifolia*, 14 Aug. 1934,

G.B. Cummins, CUP-24472; Tennessee, 0, I on *M. coronaria*, 14 Aug. 1934, G.B. Cummins, CUP-24468 & CUP-20257; Virginia, 0, I on *M. domestica*, 7 Aug. 1897, W.A. Merrill, CUP-9367; West Virginia, 0, I on *M. domestica*, 5 Aug. 1930, collector unknown, CUP-20151, CUP-20218, CUP-20223 & CUP-20231.

Host range and geographical distribution confirmed in this study — *Juniperus scopulorum* – USA; *Juniperus virginiana* – USA; *Juniperus* sp. – USA; *Malus angustifolia* – USA; *Malus coronaria* – USA; *Malus domestica* – USA; *Malus glaucescens* – USA; *Malus pumila* – USA; *Malus soulardi* – USA.

Additional host range and geographical distribution reported in previous studies — *Crataegus mollis* – USA; *Juniperus chinensis* – USA; *Juniperus chinensis* f. *globosa* – USA; *Juniperus communis* var. *depressa* – USA; *Juniperus horizontalis* – USA; *Juniperus horizontalis* f. *alpina* – USA; *Juniperus pinchotii* – USA; *Juniperus scopulorum* – Canada, USA; *Juniperus silicicola* – USA; *Juniperus utahensis* – USA; *Juniperus virginiana* var. *crebra* – Canada; *Pyrus angustifolia* – USA; *Pyrus baccata* – USA; *Pyrus coronaria* – USA; *Pyrus floribunda* – USA; *Pyrus ioensis* – USA; *Pyrus ioensis* var. *plena* – USA (Farr & Rossman 2019).

Notes — *Gymnosporangium juniperi-virginianae* was first reported on *J. virginiana* in the USA, and it is characterised by roestelioid aecia up to 1.5 mm high, rugose peridial cells and telia within a large roundish gall. This species was first described by Schweinitz (1822) on *J. virginiana* in North Carolina in USA, but no specimen information was listed in the original description. Thereafter, Farlow (1880) described it with a line drawing as *G. macropus*. Subsequent comprehensive studies of the genus *Gymnosporangium* were conducted by Kern (1911), and morphology, type locality and host information were discussed without any type specimen information. We failed to locate type materials of this species, and thus designated a neotype specimen of *G. juniperi-virginianae* based on its morphology, host and location. This species has frequently been reported in North America and Canada as causal agent of notorious rust diseases on commercial apple cultivars, and some Asian countries and the European Union list this rust fungus as one of the most important plant quarantine fungi (EPPO/CABI 1996b, EPPO 2017, 2018). Twelve *Malus* species, i.e., *M. angustifolia*, *M. baccata*, *M. coronaria*, *M. domestica*, *M. floribunda*, *M. fusca*, *M. glaucescens*, *M. ioensis*, *M. pumila*, *M. sieboldii*, *M. spectabilis* and *M. sylvestris*, were reported as aecial hosts (Farr & Rossman 2019). We confirmed seven *Malus* species as aecial hosts of this species, and two additional *Malus* species, *M. coronaria* and *M. soulardi* were reported as new aecial hosts. Thus, species boundaries, host alternations and geographic distributions of this quarantine species were confirmed.

***Gymnosporangium lachrymiforme* P. Zhao & L. Cai, sp. nov. — MycoBank MB832743; Fig. 8**

Etymology. Epithet refers to aecia with long balanoid peridia.

Typus. CHINA, Guizhou, Guiyang City, 0, I on *Malus* sp., 14 May 2015, P. Zhao (holotype HMAS248123). ITS and sequences GenBank MN605716 and MN605794.

Spermogonia, *uredinia* and *telia* not found. *Aecia* foliicolous, hypophyllous, roestelioid; peridium balanoid, 3.0–8.5 mm high, rupture and becoming lacerate at side, peridial cells oblong, 47–85 × 24–33 µm, outer walls smooth, inner walls and side walls densely verrucose with small papillae; aeciospores globoid or broadly ellipsoid, 15–29 × 14–24 µm, walls slightly brown, 2 µm thick; germ pores scattered, 3–7.

Additional material examined. CHINA, Guizhou, Guiyang City, 0, I on *Malus* sp., 14 May 2015, P. Zhao, ZP-R1448.

Host range and geographical distribution — *Malus* sp. – China.

Notes — This rust was found on one unidentified *Malus* species in China, and it was characterised by its balanoid aecia with linear and relatively shorter peridia. This species resembles *G. sabiniae* in its balanoid aecia, but the length of peridia, and

dimensions of the peridial cells clearly differentiate the two species. Among other *Gymnosporangium* species reported on *Malus*, the aecial stage of this species only resembles *G. hemisphericum* in the dimension and shape of peridial cells and aeciospores (Hiratsuka et al. 1992). However, our new species differs in the balanoid aecia with relatively long peridia. Based on these morphological and molecular differences, we proposed it as a new species.

***Gymnosporangium libocedri* (Henn.) F. Kern, Bull. Torrey Bot. Club 35: 509. 1908 — Fig. 9**

Basionym. *Phragmidium libocedri* Henn., Hedwigia 37: 271. 1898.

Synonyms. *Gymnosporangium aurantiacum* Syd. & P. Syd., Ann. Mycol. 2(1): 28. 1904, nom. inval.

Gymnosporangium blasdaleanum F. Kern, Bull. New York Bot. Gard. 7: 437. 1911.

Typus. USA, California, Potter Valley, Mendocino C, III on *Calocedrus decurrens*, 1894, A. Purpus, B17504 (holotype).

Epitypification. USA, California, Along Moro Rock Trail, Giant Forest, Sequoia National Park, III on *Calocedrus decurrens*, 10 July 1930, J.P. Tracy, HMAS49246 (epitype designated here, MBT388924). SSU, ITS and LSU sequences GenBank MN605009, MN605717 and MN605795.

Spermogonia not found. *Aecia* foliicolous, hypophyllous, roestelioid; peridium cornuted, horned, margin lacerate, spreading or recurved, 1.5–3 mm high, peridial cells rhomboid, 77–148 × 15–29 µm, outer walls and inner walls verrucose; aeciospores globose, 13–25 × 10–23 µm, walls yellowish, 1.0–1.5 µm thick, verrucose with refractive granules. *Uredinia* absent. *Telia* foliicolous, usually without distortions of the stems, but sometimes producing witches' brooms, roundish oval, 0.8–2.0 mm across, pulvinate, reddish brown; teliospores 2–5-celled, linear-oblong, 41–86 × 14–22 µm, walls 1.0–1.5 µm, pale orange to orange, pores 2, septate except apical in uppermost cells; pedicels cylindrical, 5.0–20 µm diam.

Additional materials examined. CHINA, Guizhou, 0, I on *M. sylvestris*, 26 Sept. 2016, P. Zhao, ZP-R471. – USA, Berkeley, III on *C. decurrens*, 1 June 1936, S. T. Parks, HMAS45643; California, III on *C. decurrens*, 10 July 1930, J.P. Tracy, HMAS2616; Maine, 0, I on *Malus* sp., 28 May 1939, A.E. Prince, HMAS243537, HMAS243649 & HMAS243651; Maine, III on *J. communis* var. *depressa*, 28 May 1939, A.E. Prince, HMAS43589.

Host range and geographical distribution confirmed in this study — *Calocedrus decurrens* – USA; *Juniperus communis* var. *depressa* – USA; *Malus* sp. – USA.

Additional host range and geographical distribution reported in previous studies — *Amelanchier alnifolia* – USA; *Amelanchier florida* – USA; *Amelanchier pallida* – USA; *Chaenomeles japonica* – USA; *Crataegus douglasii* – USA; *Cydonia oblonga* – USA; *Heyderia decurrens* – USA; *Juglans californica* – USA; *Malus baccata* – USA; *Malus floribunda* – USA; *Malus fusca* – USA; *Malus ioensis* – USA; *Malus sylvestris* – USA; *Pyrus communis* – USA; *Pyrus fusca* – USA; *Sorbus americana* – USA; *Sorbus aucuparia* – USA; *Sorbus hybrida* – USA (Farr & Rossman 2019).

Notes — This species was first described on *Calocedrus decurrens* in California, USA, and it is characterised by its verrucose aeciospores with refractive granules, 2–5-celled teliospores with terete pedicels up to 20 µm diam (Arthur 1934, Kern 1973). Hennings (1900) first described it on *Calocedrus decurrens* as *Phragmidium libocedri*, and later Sydow & Sydow (1904) proposed a new name *G. aurantiacum* Syd. & P. Syd. based on specimens collected from the same host and regions. Although he treated *Phragmidium libocedri* as synonym of *G. aurantiacum* Syd. & P. Syd., this name is invalid because it was already occupied (Chevallier 1826). After examination of these specimens, Kern (1908) proposed a combination *G. libocedri*, and further treated *Phragmidium libocedri* as synonym. Here we selected a specimen as epitype of *G. libocedri*. The information of species identity, host alternation and geographic distribution of this species was further clarified and host alternation from *Calocedrus* and *Malus* species was confirmed in our study, which was previously known based on inoculation tests conducted by Kern (1911). In the previous

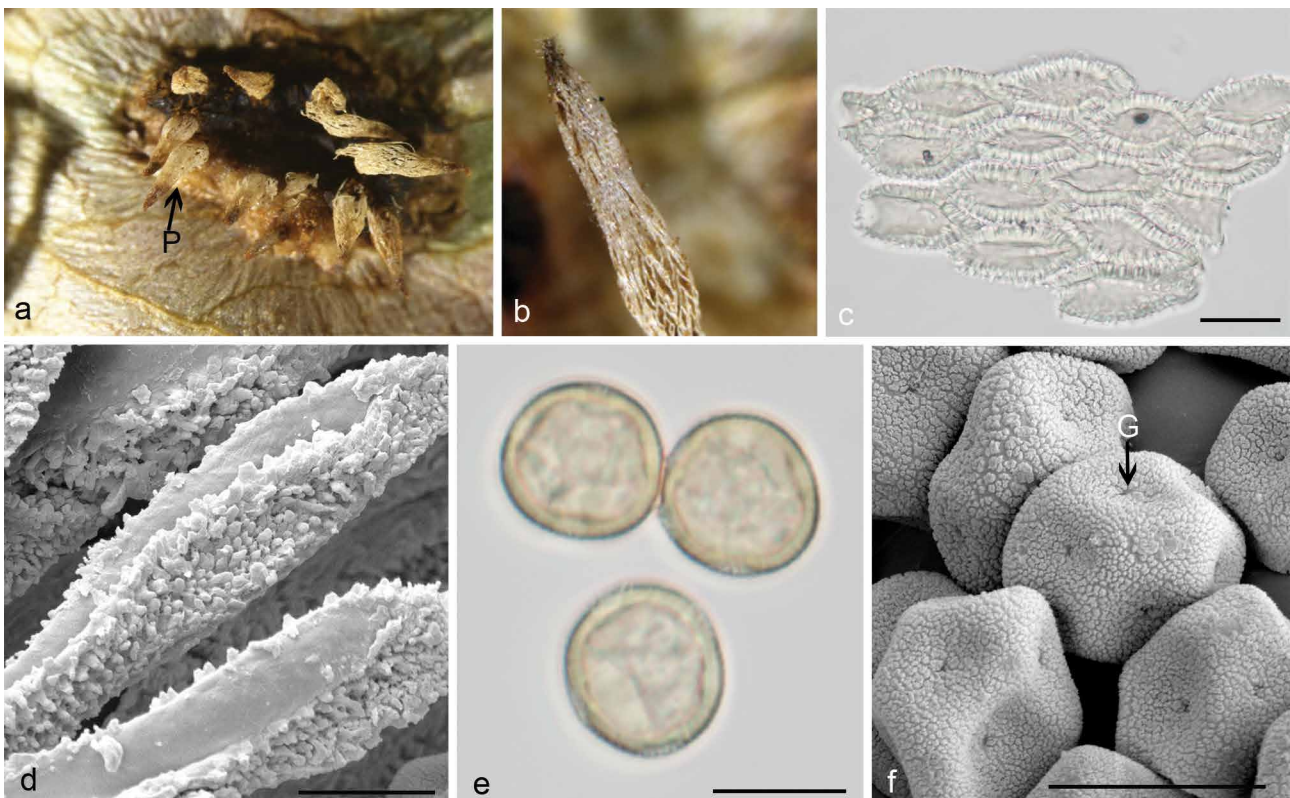


Fig. 8 Morphology of *G. lachrymiforme*. a. Aecia with balanoid peridia (P) on the hypophyllous leaf surface; b. peridium with cornuted apex; c. oblong peridial cells observed by LM; d. ultrastructure of peridial cells observed by SEM; e. globose or ellipsoid aeciospores with scattered germ pores (G) observed by LM; f. ultrastructure of aeciospores observed by SEM. — Scale bars: c–f = 20 µm.

study, *M. angustifolia*, *M. fusca* and *M. ioensis* were reported as aecial hosts, and here we further confirmed one additional telial host, *J. communis* var. *depressa*.

Gymnosporangium miyabei G. Yamada & I. Miyake, Bot. Mag. (Tokyo) 22: 23. 1908

Synonyms. *Roestelia solenoides* Dietel, Bot. Jahrb. Syst. 32: 631. 1903.
Roestelia solitaria Miyabe, Bot. Mag. (Tokyo) 17: 34. 1903.

Gymnosporangium solenoides F. Kern, Bull. New York Bot. Gard. 7: 450. 1911.

Spermogonia not found. *Aecia* foliicolous, hypophyllous, roestelioid, borne on frustum-like protuberances; peridia cornute form, dehiscent at apex, not becoming much lacerate 2.5–5.0 mm high, peridial cells rhomboid, 52–109 × 15–33 μm, outer walls smooth, inner walls densely verrucose, with small oval or irregular papillae; aeciospores globose, 15–27 × 10–23 μm, walls yellowish, 1.0–1.5 μm thick, large verrucose, granules on surface up to 1.6 μm, two or more gathered. *Uredinia* absent. *Telia* caulicolous, on fusiform or irregular swellings with knotty rough surface, pulvinate, applanate, or somewhat wart-like; teliospores chiefly 2-celled, occasionally with 1 or 3 cells, nar-



Fig. 9 Morphology of *G. libocedri*. a. Aecia (A) on the hypophyllous leaf surface; b. linear-rhomboid peridial cells observed by LM; c. ultrastructure of peridial cells observed by SEM; d. globose or ellipsoid aeciospores with scattered germ pores observed by LM; e. ultrastructure of aeciospores with apparent germ pores (G) observed by SEM; f. foliicolous telia (T); g. 2-celled and pedicellate teliospores with cylindrical and hyaline pedicels; h. 3- or 4-celled teliospores observed by LM. — Scale bars: b–c = 50 μm; d–e, g–h = 20 μm.

rowly ellipsoid, 34–89 × 14–23 µm, walls 1–3.5 µm, brownish, pores usually 1 in a cell apical, sometimes near the septum in the upper cell, pedicels cylindrical, 3.0–4.5 µm diam.

Additional materials examined. CHINA, Jiangsu, Nanjing, III on *J. chinensis*, 5 Apr. 1932, F.L. Tai, HMAS11150; Jiangsu, Nanjing, 0, I on *M. spectabilis*, 22 Sept. 1928, F.L. Tai, HMAS11186 & HMAS11201; Shaanxi, Wugong, III on *J. chinensis* var. *kaizuca*, 16 Apr. 1940, S.E. Liu, HMAS22178. – FINLAND, Nyland, 0, I on *M. sylvestris*, 8 Sept. 1912, S. Salmenlinna, HMAS70746; Nyland, 0, I on *M. sylvestris*, 1 Sept. 1949, H.H. Roivainen, CUP-56156.

Hosts range and geographical distribution confirmed in this study — *Chamaecyparis pisifera* – Japan; *Juniperus chinensis* – China; *Juniperus* sp. – USA; *Malus sylvestris* – Finland.

Additional host range and geographical distribution reported in previous studies — *Chamaecyparis pisifera* – Japan; *Chamaecyparis pisifera* var. *plumosa* – Japan; *Chamaecyparis pisifera* var. *squarrosa* – Japan; *Micromeles alnifolia* – Japan; *Micromeles japonica* – Japan; *Pyrus miyabei* – Japan; *Sorbus alnifolia* – Japan, South Korea; *Sorbus commixta* – Japan; *Sorbus japonica* – Japan (Farr & Rossman 2019).

Notes — This species was first reported from Japan with its telial host on *Chamaecyparis pisifera*, and aecial hosts on *Micromeles alnifolia* and *M. japonica* (Yamada & Miyake 1908). This rust is characterised by the dimensions of its peridial cells, aeciospores with large verrucose ornamentations and densely verrucose peridial cells. In addition, it has 1–3-celled teliospores with cylindrical pedicels. Here we confirmed the host alternation of this species between *Chamaecyparis*, *Juniperus* and *Malus*, and the species delineation and geographic distribution of this species was clarified.

Gymnosporangium monticola H.Y. Yun, Mycologia 101: 803. 2009

Typus. SOUTH KOREA, Gyeonggi, Gwacheon, III on *J. rigida*, 10 Apr. 2001, H.Y. Yun, HKFRI-2018 (holotype).

Spermogonia not found. *Aecia* foliicolous, fructicolous, roestelioid; peridium cornuted, rupturing and lacerate, 0.5–3.0 mm high, peridial cells roundish rhomboid, 42–93 × 14–22 µm long, outer walls smooth, inner walls with small papillae; aeciospores globose or ovoid, 16–31 × 14–26 µm, walls yellow-brown, 1.0–2.5 µm thick, minutely coronate. *Uredinia* absent. *Telia* caulicolous, forming irregularly fusiform swellings of smaller branches, applanate or pulvinate, dark brown, 14–55 µm; teliospores 2–3-celled, broadly ellipsoid, 28–55 × 15–31 µm, walls orange, with thin-walled, 1.4–2.8 µm thick, 1–2 pores near septum or 1 apical in upper cell; pedicels cylindrical, 2.0–4.5 µm diam.

Additional materials examined. CHINA, Sichuan, Wolong, 0, I on *M. kansuensis*, 23 Sept. 1982, Y.C. Wang, HMAS44514. – JAPAN, Shizuoka, III on *J. rigida*, 1 Apr. 1924, M. Hara, HMAS11145.

Host range and geographical distribution confirmed in this study — *Juniperus rigida* – Japan, South Korea; *Malus kansuensis* – China; *Sorbus alnifolia* – South Korea.

Notes — *Gymnosporangium monticola* was first described on *J. rigida* in South Korea, and this species resembles *G. cornutum* but differs in the size of aecia, shape of peridial cells, dimensions of peridial cells and morphology of its telial and teliospores (Yun et al. 2009). It was described with *S. alnifolia* as aecial host and *J. rigida* as telial host. Based on our morphological and molecular studies, host alternation was confirmed, and *M. kansuensis* was reported as a new aecial host.

Gymnosporangium nelsonii Arthur, Bull. Torrey Bot. Club 28: 665. 1901 — Fig. 10

Synonyms. *Aecidium nelsonii* (Arthur) Farl., Bibliogr. Index N. Amer. Fungi 1(1): 68. 1905.

Gymnosporangium durum F. Kern, Bull. Torrey Bot. Club 34: 460. 1907.

Typus. USA, Wyoming, Laramie Hills, *J. scopulorum*, 10 May 1895, A. Nelson, NYBG638372 (isotype, designated as lectotype here, MBT388925). SSU, ITS and LSU sequences GenBank MN642599, MN642594 and MN642618.

Spermogonia not found. *Aecia* foliicolous, occasionally fructicolous, roestelioid; peridium cornuted, rupturing by few longitudinal slits along sides, 2.5–5.0 mm high, peridial cells linear-rhomboid, 55–106 × 18–32 µm long, outer cells smooth, inner walls densely rugose with elongate small papillae; aeciospores globose or ovoid, 18–31 × 14–26 µm, walls yellow-brown, 2.0–2.5 µm thick, densely verrucose. *Uredinia* absent. *Telia* caulicolous, on globoid galls up to 28 mm diam, cylindrical-cornute, sometimes wedge-shaped, irregularly compressed; teliospores 2-celled, narrowly or broadly ellipsoid, 38–69 × 20–33 µm, walls orange, with thin-walled, 0.5–2.5 µm thick, pore 1 or 2 per cell at septum, pedicel cylindrical, hyaline, 5.0–9.5 µm diam.

Additional materials examined. CANADA, Ontario, Algoma, 0, I on *Amelanchier* sp. 15 Sept. 1972, J.A. Parmelee, NYBG212838. – USA, New York, 0, I on *A. alnifolia*, 25 Aug. 1986, collector unknown, NYBG3009186; New York, 0, I on *Peraphyllum ramosissimum*, 11 July 1993, C.T. Rogerson, NYBG NYBG3009187; Illinois, Kane County, 0, I on *Peraphyllum ramosissimum*, 26 Aug. 1994, C.T. Rogerson, NYBG3009190; Illinois, Kane County, III on *J. scopulorum*, 11 May 1990, C.T. Rogerson, NYBG3009191; Utah, San Juan College, III on *J. utahensis*, 13 May 1945, A.S. Rhoads, CUP-65684; Utah, Weber, III on *J. scopulorum*, 7 May 1987, C.T. Rogerson, NYBG3009188.

Host range and geographical distribution confirmed in our studies — *Amelanchier alnifolia* – USA; *Amelanchier* sp. – Canada; *Juniperus scopulorum* – Canada, USA; *Juniperus utahensis* – USA; *Peraphyllum ramosissimum* – USA.

Additional host range and geographical distribution reported in previous studies — *Amelanchier alnifolia* – Canada; *Amelanchier alnifolia* var. *cusickii* – Canada, USA; *Amelanchier alnifolia* var. *semiintegrifolia* – Canada; *Amelanchier bakeri* – USA; *Amelanchier cusickii* – Canada; *Amelanchier florida* – USA; *Amelanchier goldmanii* – USA; *Amelanchier huronensis* – Canada; *Amelanchier intermedia* – Canada; *Amelanchier laevis* – Canada; *Amelanchier mormonica* – USA; *Amelanchier oreophila* – USA; *Amelanchier polycarpa* – USA; *Amelanchier pumila* – USA; *Amelanchier sanguinea* – Canada; *Amelanchier utahensis* – USA; *Crataegus oxyacantha* – USA; *Cydonia oblonga* – USA; *Cydonia vulgaris* – USA; *Juniperus californica* – USA; *Juniperus deppeana* – USA; *Juniperus flaccida* – USA; *Juniperus horizontalis* – Canada, USA; *Juniperus monosperma* – USA; *Juniperus occidentalis* – USA; *Juniperus osteosperma* – USA; *Malus diversifolia* – USA; *Malus fusca* – USA; *Malus rivularis* – USA; *Pyrus communis* – USA; *Pyrus diversifolia* – USA; *Pyrus fusca* – USA; *Sorbus occidentalis* – USA; *Sorbus scopulina* – USA; *Sorbus sitchensis* – USA (Farr & Rossman 2019).

Notes — *Gymnosporangium nelsonii* was first reported on *J. scopulorum* in the USA. The connection with its aecial host *Amelanchier* was confirmed in the early 20th century (Arthur 1934). The taxonomic status of this species in relation to *G. corniculans* has been considered dubious for a long time. Here we confirmed the phylogenetic distinction of the two species by employing morphological and sequence data from a lectotype specimen, which support these two taxa as independent species. Hitherto, three *Malus* species, *M. diversifolia*, *M. fusca* and *M. rivularis* were reported as aecial hosts of *G. nelsonii* (Farr & Rossman 2019). We confirm the host alternation of *G. nelsonii* on *Amelanchier* and *Juniperus*, and another aecial host, *Peraphyllum ramosissimum*, was confirmed as a new aecial host.

Gymnosporangium nidus-avis Thaxt., Connecticut Agric. Exp. Sta. Bull. 107: 6. 1891 — Fig. 11

Synonyms. *Puccinia nidus-avis* (Thaxt.) Kuntze, Revis. Gen. Pl. (Leipzig) 3(3): 507. 1898.

Tremella nidus-avis (Thaxt.) Arthur, Proc. Indiana Acad. Sci.: 136. 1901. *Gymnosporangium juvenescens* F. Kern, Bull. New York Bot. Gard. 7: 448. 1911.

Typus. USA, Connecticut, 0, I on *A. canadensis*, 11 June 1889, *R. Thaxter*, CUP-227 (isotype). SSU, ITS and LSU sequences GenBank MN605014, MN605719 and MN605797.

Spermogonia not found. *Aecia* hypophyllous, foliicolous, fructicolous and caulicolous, roestelioid; peridium cylindrical, lacerate along sides, 2.0–4.5 mm high, peridia cells rhomboid, 55–94 × 15–27 μm long, outer cells smooth, inner walls densely rugose; aeciospores globose or ovoid, 22–35 × 16–26 μm, walls yellow-brown, 2.0–3.5 μm thick, densely verrucose. *Uredinia* absent. *Telia* caulicolous, brush-like witches' broom or birds' nests, ligulate or pulvinate; teliospores 2-celled, oc-

asionally 1–4-celled, 34–55 × 16–27 μm, walls orange, with thin-walled, 1.0–2.5 μm thick, pore 1 or 2 per cell at septum, pedicel cylindrical, hyaline, 3.5–7.5 μm diam.

Additional materials examined. USA, Arizona, Coconino County, 0, I on *A. utahensis*, 27 Aug. 1994, *C.T. Rogerson*, NYBG3009270; New Jersey, Monmouth County, 0, I on *M. communis*, 6 May 1984, *C.T. Rogerson*, NYBG461234; New York, Bruce, III on *J. horizontalis*, 20 May 1957, *R.F. Cain*, NYBG33324; New York, Bruce, III on *J. virginiana*, 6 May 1984, *W.R. Buck*, NYBG3011033; New York, Tompkins, Ithaca, III on *Juniperus* sp., 17 Mar. 1905, *V.H. James*, CUP-19416; Utah, Cache County, 0, I on *A. alnifolia*, 18 Aug. 1940, *C.T. Rogerson*, NYBG3009399.

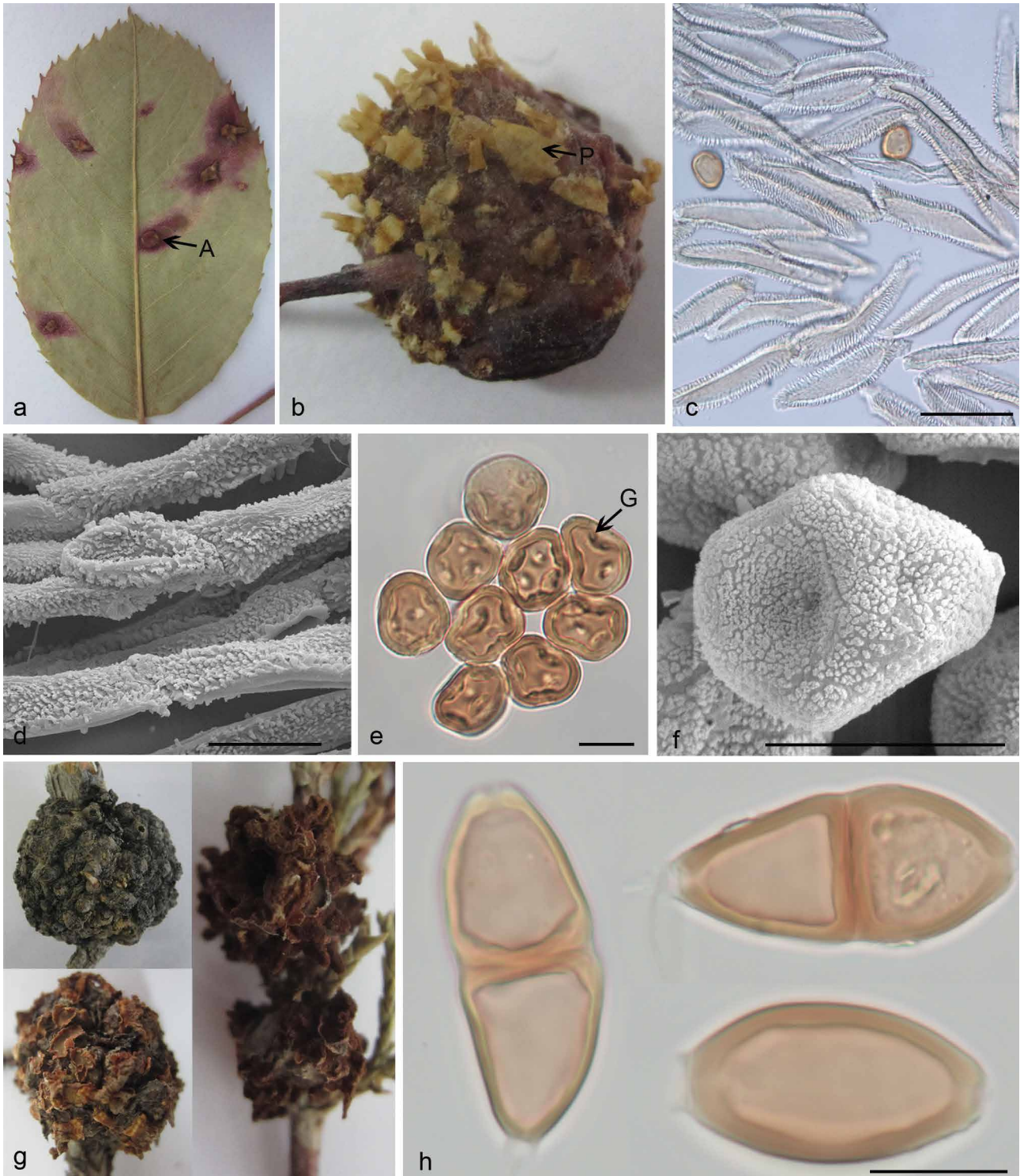


Fig. 10 Morphology of *G. nelsonii*. a. Aecia (A) on the hypophyllous leaf surface; b. aecia with yellowish peridia (P) on the fruit; c. linear-rhomboid peridial cells observed by LM; d. ultrastructure of peridial cells observed by SEM; e. globose or ellipsoid aeciospores with scattered germ pores (G) observed by LM; f. ultrastructure of aeciospores observed by SEM; g. telia on the stem with globoid galls formation; h. 1- or 2-celled and pedicellate teliospores observed by LM. — Scale bars: c–d = 50 μm; e–f, h = 20 μm.

Host range and geographical distribution confirmed in this study — *Amelanchier alnifolia* – USA; *Amelanchier canadensis* – USA; *Malus communis* – USA; *Juniperus horizontalis* – USA; *Juniperus virginiana* – USA.

Additional host range and geographical distribution reported in previous studies — *Amelanchier alnifolia* – Canada; *Amelanchier alnifolia* var. *semi-integrifolia* – Canada; *Amelanchier canadensis* – Canada; *Amelanchier cusickii* – Canada; *Amelanchier florida* – Canada; *Amelanchier huronensis* – Canada; *Amelanchier intermedia* – Canada, USA; *Amelanchier laevis* – Canada, USA; *Amelanchier mormonica* – USA; *Amelanchier oblongifolia* – USA; *Amelanchier stolonifera* – USA; *Amelanchier utahensis* – USA; *Amelanchier vulgaris* – USA; *Cydonia oblonga* – USA; *Cydonia vulgaris* – USA; *Juniperus chinensis* – South Korea; *Juniperus horizontalis* – Canada;

Juniperus scopulorum – USA; *Juniperus silicicola* – USA; *Juniperus virginiana* – Canada; *Malus sylvestris* – USA (Farr & Rossman 2019).

Notes — This species was initially described by Thaxter (1891), with the aecial stage first reported on *A. canadensis* and telial stage on *J. virginiana* (Farlow 1906, Parmelee 1979). It is characterised by producing brush-like witches' broom or birds' nests telia and 1–4-celled teliospores with terete pedicels. We successfully generated rDNA sequence data from the isotype specimen, and further confirmed taxonomic identity, host alternation and geographic distribution of this species. Here, one new aecia host of *G. nidus-avis*, i.e., *M. communis*, is reported for the first time.



Fig. 11 Morphology of *G. nidus-avis*. a. Label of type specimen and aecia (A) on the hypophyllous leaf surface; b. aecia with peridia (P) on the hypophyllous leaf surface; c. aecia (A) on the fruit; d. linear-rhomboid peridial cells observed by SEM; e. globose or ellipsoid aeciospores with scattered germ pores observed by LM; f. ultrastructure of aeciospores observed by SEM; g. foliicolous telia (T) with pulvinate sori; h. 2-celled and pedicellate teliospores with cylindrical and hyaline pedicels, occasionally with 1- or 3-celled teliospores. — Scale bars: d = 50 µm; e–f, h = 20 µm.

Gymnosporangium shennongjiaense P. Zhao & L. Cai, *sp. nov.* — MycoBank MB832744; Fig. 12

Etymology. Epithet refers to the locality where the type specimen was collected.

Typus. CHINA, Hubei, Shennongjia, 0, I on *M. asiatica*, 9 Sept. 1984, L. Guo (holotype HMAS55353). SSU, ITS and LSU sequences GenBank MN605025, MN605723 and MN605801.

Spermogonia, uredinia and *telia* not found. *Aecia* hypophyllous, roestelioid, foliicolous and caulicolous, 0.5–2.0 mm high; peridium cylindrical, becoming fimbriate, peridial cells rhomboid-oblong, 69–105 × 33–51 μm, outer walls smooth, inner walls verruculose with ridge-like papillae; aeciospores globoid, large coronate, 27–49 × 24–37 μm, walls yellowish, 2.0–5.0 μm thick.

Additional materials examined. CHINA, Guizhou, Guiyang City, 0, I on *Malus* sp., 14 May 2015, P. Zhao, ZP-R511; Sichuan, Guangyuan, Huaying, Tianchi, 0, I on *M. asiatica*, 21 May 2016, P. Zhao, ZP-R420.

Hosts range and geographical distribution — *Malus asiatica* – China; *Malus* sp. – China.

Notes — This novel species differs from other *Gymnosporangium* species but resembles *G. clavipes* in aecial morphology, such as the dimension of peridial cells and aeciospores, position of aecia and peridia. Detailed morphological comparison indicated that the ornamentation of peridial cells and aeciospores can differentiate the two species. *Gymnosporangium shennongjiaense* has peridial cells with a verruculose inner walls, which differs from the tuberculate inner walls of *G. clavipes*. It also has aeciospores with large coronate walls, while *G. clavipes* has echinulate aeciospores. Molecular data further supported the

phylogenetic distinction of the two species (Fig. 2). This novel species is found on *M. asiatica* and one unidentified *Malus* species in the southwest part of China, but its telial host is still unknown.

Gymnosporangium spinulosum P. Zhao & L. Cai, *sp. nov.* — MycoBank MB832745; Fig. 13

Etymology. Epithet refers to special spines on the surface of peridia and aeciospores.

Typus. CHINA, Sichuan, Chengdu, 0, I on *M. spectabilis*, 19 May 1955, Y.C. Wang (holotype HMAS26416). SSU, ITS and LSU sequences GenBank MN605030, MN605727 and MN605805.

Spermogonia, uredinia and *telia* not found. *Aecia* foliicolous, hypophyllous, roestelioid, 4–9 mm high, tubular; peridium cornuted, rupturing at apex, peridial cells rhomboid or oblong, 55–86 × 14–23 μm, outer cells rugose, inner walls densely verrucose with long papillae up to 5 μm; aeciospores globoid, 14–25 × 13–22 μm, walls slightly brown, 2 μm thick, evenly thickened, walls large coronate, basal parts columnar and upper parts separated into several long protuberances.

Additional materials examined. CHINA, Jiangsu, Suzhou, 0, I on *M. spectabilis*, 7 Sept. 1929, H.T. Chang, HMAS11219.

Host range and geographical distribution — *Malus spectabilis* – China.

Notes — This species is characterised by its special ornamentation in peridial cells and aeciospores. In addition, it has relatively small aeciospores. Compared to other *Gymnosporangium* species, it resembles *G. asiaticum* in the dimension of its aeciospores, and the two species have commonly been

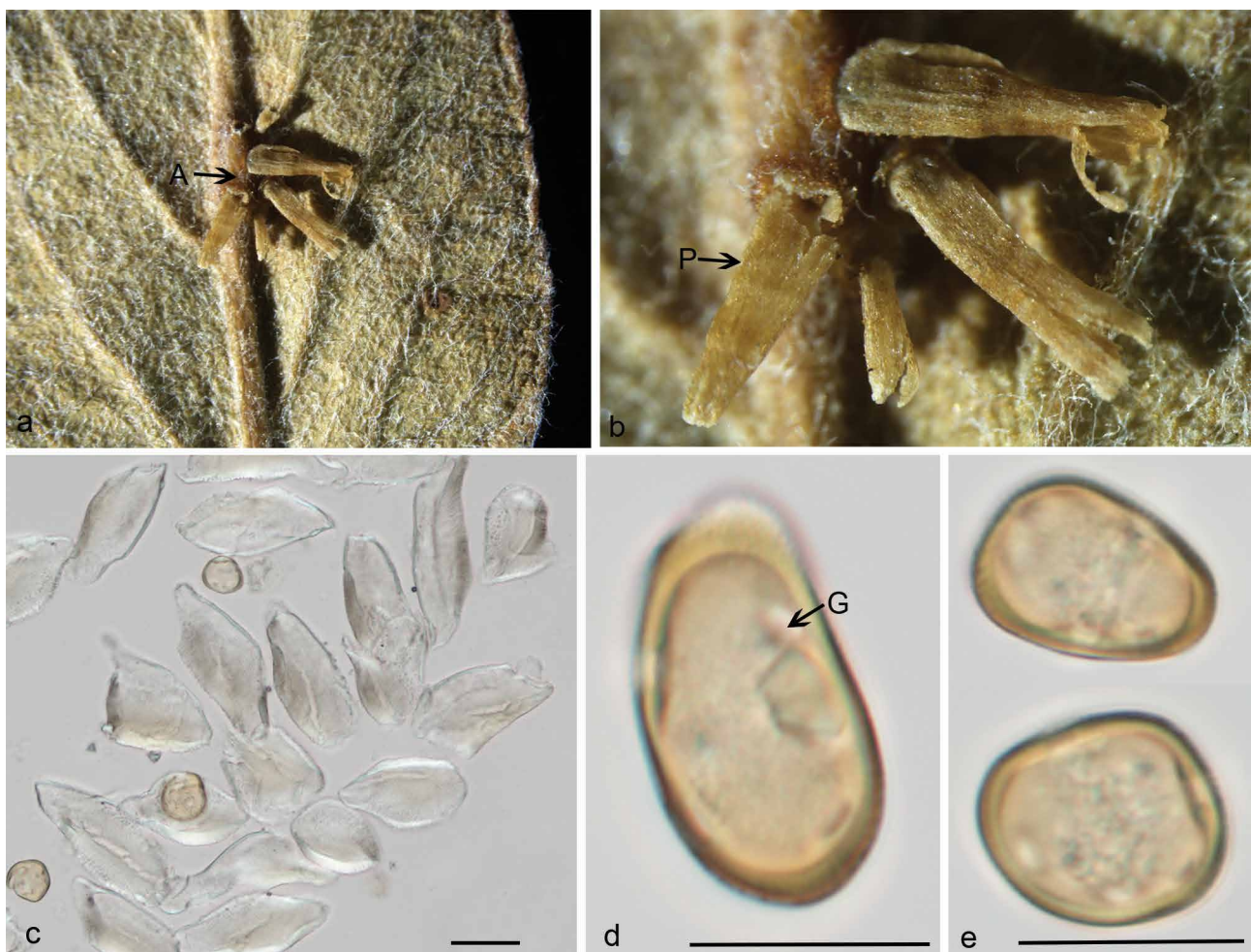


Fig. 12 Morphology of *G. shennongjiaense*. a. Aecia (A) on the hypophyllous leaf surface; b. peridia (P) on the hypophyllous surface of leaf; c. oblong peridial cells with apparently thickened side walls; d. ellipsoid aeciospores with apparently thickened apex; e. globoid or ellipsoid aeciospores with scattered germ pore (G). — Scale bars: c–e = 20 μm.

confused in the past (Wang & Guo 1985, Zhuang 2012). However, these two species clearly differ in ornamentation of peridial cells and aeciospores. This novel species has peridial cells with papillae up to 5 µm long, which clearly differs from those in *G. asiaticum*. Besides, it has aeciospores with basal parts columnar and upper parts separated into several long protuberances, and this character can clearly differentiate the two species. Phylogenetic results further supported this species distinct from *G. asiaticum* and other species.

***Gymnosporangium tiankengense* P. Zhao & L. Cai, sp. nov.**
— MycoBank MB832746; Fig. 14

Etymology. Epithet refers to the locality where the type specimen was collected.

Typus. CHINA, Guangxi, Bai Se, Leye County, Shenmu Tiankeng, 0, I on *Malus* sp., 18 June 2017, P. Zhao (holotype HMAS248124). SSU, ITS and LSU sequences GenBank MN605026, MN605725 and MN605803.

Spermogonia, *uredinia* and *telia* not found. *Aecia* foliicolous, hypophyllous, roestelioid; peridium tubular, spreading or erect, 3–8.5 mm high, peridial cells rhomboid-oblong, 34–77 × 17–32 µm, outer walls smooth, inner walls small papillae and side walls moderately rugose; aeciospores globoid, ovoid, large coronate, 16–24 × 14–20 µm, walls yellowish, 1.0–2.0 µm thick, germ pore 3–7, scattered.

Additional materials examined. CHINA, Guangxi, Bai Se, Leye County, Shenmu Tiankeng, 0, I on *Malus* sp., 18 June 2017, P. Zhao, ZP-R1375.

Host range and geographical distribution — *Malus* sp. — China.

Notes — This species is characterised by its relatively smaller peridial cells and aeciospores. Aecial morphological differences of this rust were distinct from other *Gymnosporangium* species on *Malus* species, except *G. libocedri* (Kern 1973). Based on our morphological comparison, *G. libocedri* has relatively short peridia on aecia, and large peridial cells

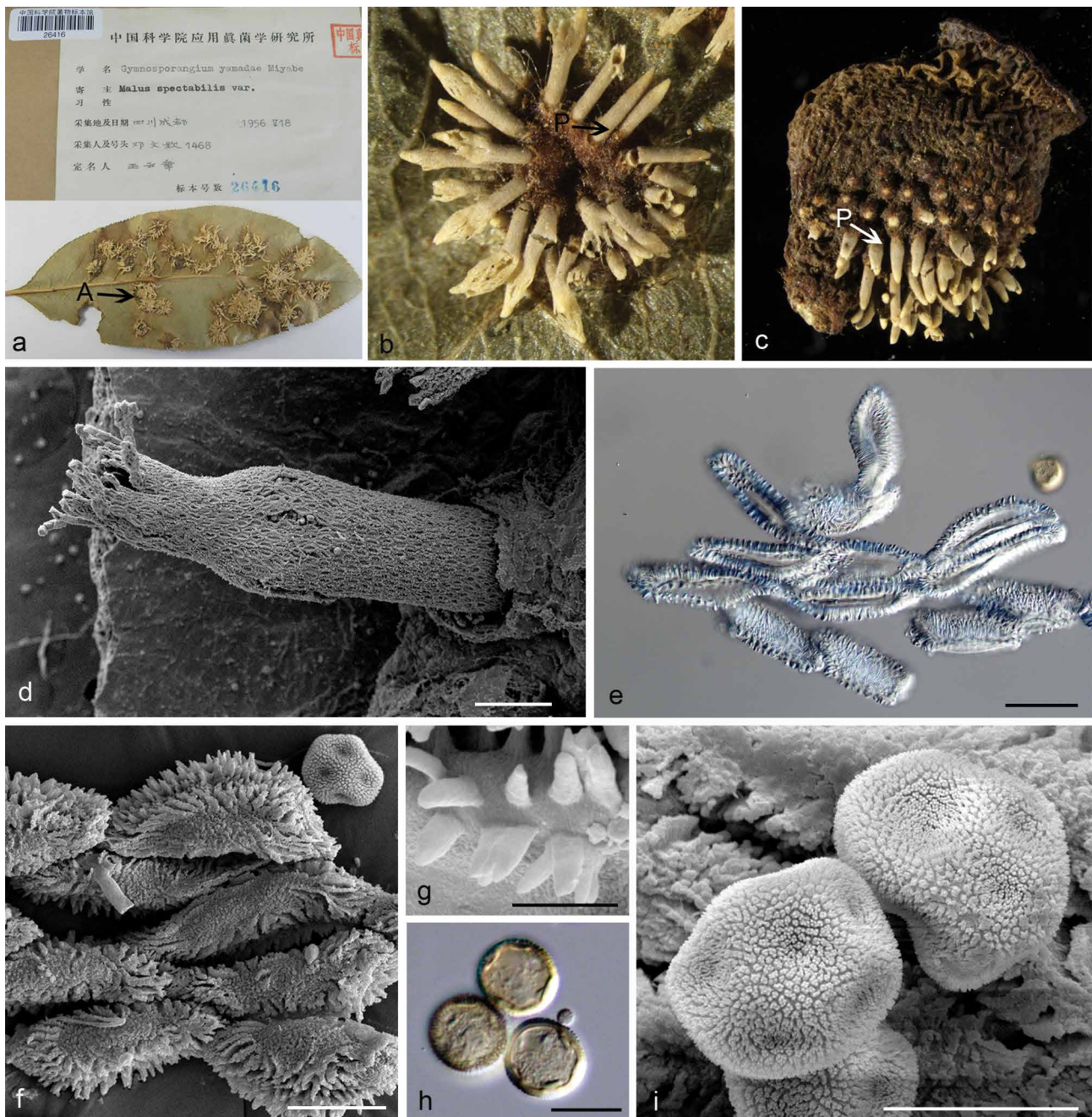


Fig. 13 Morphology of *G. spinulosum*. a. Labels of the holotype specimen and aecia (A) on the hypophyllous leaf surface; b. peridia (P) on the hypophyllous surface of leaf; c. peridia (P) on the fruit; d. ultrastructure of peridium observed by SEM; e. rhomboid peridial cells observed by LM; f. ultrastructure of peridial cells with long papillae; g. long papillae on peridial cell surface observed by SEM; h. globoid or ellipsoid aeciospores with scattered germ pore (G); i. verrucose aeciospores observed by SEM. — Scale bars: d = 200 µm; e–f, h–i = 20 µm; g = 5 µm.

(77–148 × 15–29 μm), which clearly differs from our newly proposed species. The ornamentation of aeciospores in *G. libocedri* is verrucose with refractive granules and its peridial cells with verrucose outer walls and inner walls. In addition, this new species resembles to *G. shennongjiaense* but differs in length of peridia, dimension of peridial cells and aeciospores. These morphological characters can clearly differentiate the two species, and molecular data further supported the phylogenetic distinction of this species from other *Gymnosporangium* species. This species was discovered at the edges of Tiankeng in Guangxi province in southwest part of China.

Gymnosporangium tremelloides R. Hartig, Lehrb. Kaumkrankh. 55. 1882

Spermogonia not found. *Aecia* hypophyllous, foliicolous, roestelioid; peridium cylindrical, becoming fimbriate to base, twisted or spreading, 0.5–2.5 mm high, peridial cells rhomboid, 62–105 × 16–24 μm long, outer cells smooth, inner walls rugose, with irregular ridges, roundish or irregular ridge-like papillae interspersed; aeciospores globose or ovoid, 33–45 × 26–36 μm, walls yellow-brown, 2.0–3.5 μm thick, densely echinulate. *Uredinia* absent. *Telia* caulicolous on fusiform or gall-like swellings of small branches, applanate, becoming tremelloid or patelliform; teliospores 2-celled, ellipsoid, 35–75 × 16–28 μm, walls orange, with thin-walled, 1.0–2.5 μm thick, 2–3 pores, 2 pores in lower cell near the septum and 1 sometimes in apical walls, pedicel cylindrical, hyaline, 2.5–3.5 μm diam.

Materials examined. FINLAND, Kerava Alikeraava, Harjula, 0, I on *M. baccata* var. *mandshurica*, J. Roivainen, CUP-56396; AI, Kökar Lindö, 0, I on *M. silvestris*, 1 Sept. 1949, H. Roivainen, CUP-56165. — USA, Wyoming, Albany County, III on *J. communis*, 7 June 1993, W.R. Buck, NYBG23203.

Host range and geographical distribution confirmed in this study — *Malus baccata* – Norway; *Malus domestica* – Bulgaria, Denmark, Finland, Norway, Poland, Sweden; *Malus silvestris* – Bulgaria, Denmark, Finland, Norway, Poland, Sweden, Turkey.

Additional host range and geographical distribution reported in previous studies — *Crataegus oxyacantha* – Norway; *Crataegus sanguinea* var. *chlorocarpa* – Norway; *Crataegus succulenta* – Norway; *Cydonia oblonga* – Norway, Sweden; *Juniperus communis* – Canada, Denmark, Finland, France, Germany, Norway, Poland, Sweden, Turkey, USA; *Juniperus communis* subsp. *nana* – Poland; *Juniperus communis* var. *montana* – Canada, USA; *Juniperus sibirica* – Russia; *Malus baccata* – Sweden; *Malus domestica* – Bulgaria, Denmark, Finland, Norway, Poland, Sweden, Turkey; *Malus sylvestris* – Denmark, Finland, Germany, Norway, Poland, Sweden, Turkey; *Pyrus communis* – Turkey; *Sorbus aria* – Bulgaria, Denmark, Germany, Norway, Poland, Sweden, Turkey; *Sorbus aucuparia* – Sweden, Turkey; *Sorbus chamaemespilus* – Germany; *Sorbus dumosa* – USA; *Sorbus hupehensis* – China; *Sorbus koehneana* – China; *Sorbus obtusifolia* – Norway; *Sorbus occidentalis* – Canada; *Sorbus rehderiana* – China; *Sorbus rupicola* – Norway; *Sorbus scopulina* – Canada; *Sorbus sitchensis* – Canada; *Sorbus sitchensis* var. *grayii* – Canada; *Sorbus sitchensis* var. *sitchensis* – Canada (Farr & Rossman 2019).

Notes — *Gymnosporangium tremelloides* was validly described instead of the name *G. juniperinum*, which epithet was recognized as a *nomen ambiguum* (Kern 1973). This species is characterised by its relatively larger aeciospores and peridial cells with rugose inner walls, tremelloid telia, and it is widely distributed in Africa, Asia, North America and Europe (Farr & Rossman 2019). This species was reported with its aecial stage on three *Malus* species and several *Pyrus* and *Sorbus* species, and its telial stage was reported on *J. communis* and *J. sibirica* (Crowell 1940, Kern 1973). Here we confirmed its aecial stage on three *Malus* species, and host alternation was verified by molecular data.

Gymnosporangium yamadae Miyabe ex G. Yamada, Shokubutse Byorigaku (Pl. Path) Tokyo Hakubunkwan 379: 306. 1904 — Fig. 15

Synonym. *Gymnosporangium yamadae* Miyabe, Bot. Mag. (Tokyo) 17: 34. 1902, nom. inval.

Gymnosporangium yamadae (Miyabe) Kern, Bull. New York Bot. Gard. 7: 466. 1911.

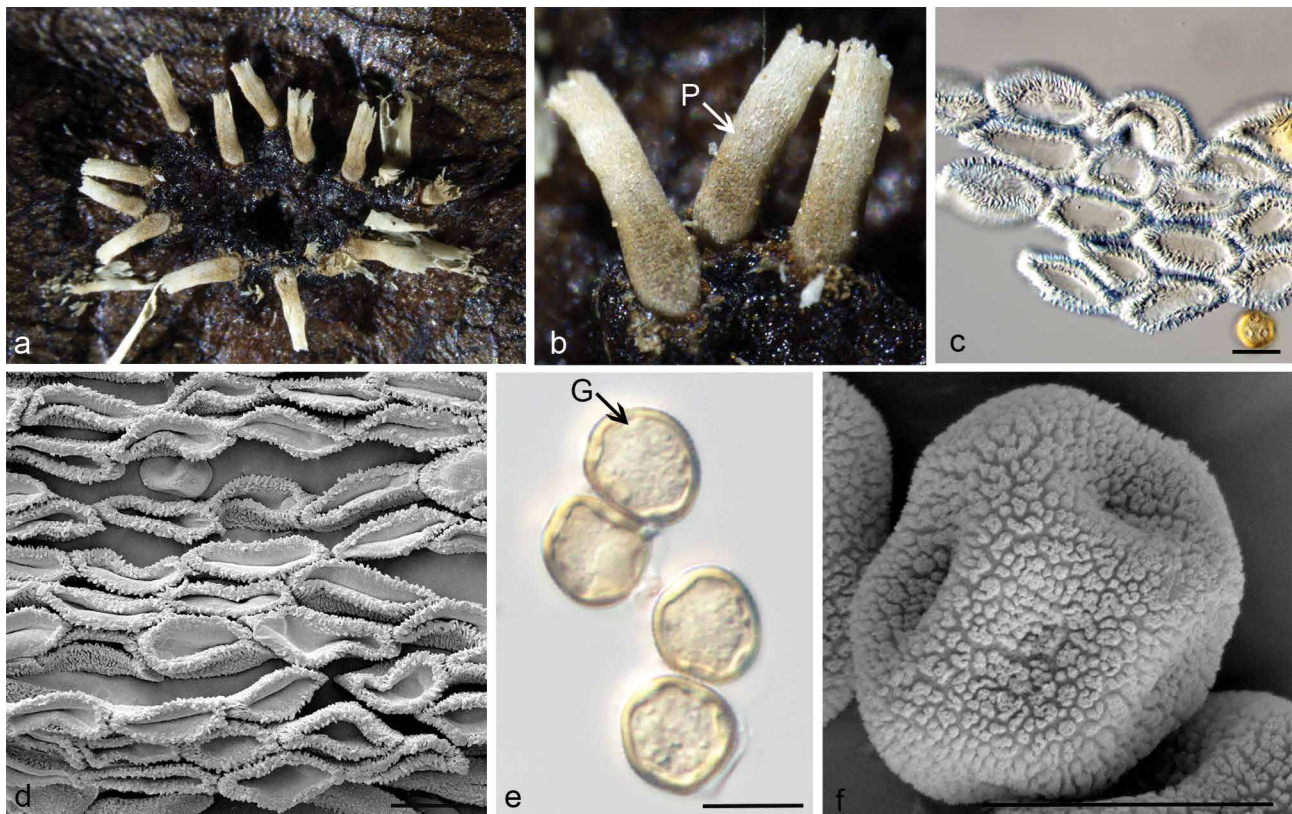


Fig. 14 Morphology of *G. tiankengense*. a. Aecia on the hypophyllous leaf surface; b. erect peridia (P) on the hypophyllous leaf surface; c. oblong peridial cells observed by LM; d. ultrastructure of peridial cells observed by SEM; e. globose or ellipsoid aeciospores with scattered germ pores (G) observed by LM; f. verrucose aeciospores observed by SEM. — Scale bars: c–f = 20 μm.

Typus. JAPAN, Hokkaido, Sapporo-shi, 0, I on *M. domestica*, III on *J. chinensis*, K. Miyabe (lectotype designated here, MBT389911, Yamada (1904: 306 (0, I, III), f. 38).

Epitypification. JAPAN, Aomori, Mutsu, Kuroshi, 0, I on *M. domestica*, 30 July 1913, M. Miura, NYBG2584 (epitype designated here, MBT389912). SSU, ITS and LSU sequences GenBank MN605048, MN605735 and MN605813.

Spermogonia not found. *Aecia* hypophyllous, foliicolous, rosetteloid, 3–6 mm high; peridium cornuted, rupturing in a lace-like network along the sides, peridial cells linear-rhomboid, 55–131 × 16–34 µm, verrucose with long papillae, outer walls smooth,

inner and side walls sparsely echinulate; aeciospores globose or ovoid, 17–27 × 16–26 µm, walls dark yellow, 1.5–2.5 µm thick, with small coronate. *Uredinia* absent. *Telia* foliicolous, or caulicolous, on globose swellings or small galls up to 9 mm high; teliospores 2-celled, ellipsoid or obovoid, 31–56 × 15–28 µm, walls 1.0–2.7 µm, pale orange to orange, pores 2 near septum or 1 apical in upper cell, frequently with an obtuse hyaline papilla at apex, pedicel cylindrical, hyaline, 2.5–3.5 µm diam.

Additional materials examined. CHINA, Beijing, 0, I on *M. baccata*, 19 Sept. 1992, S.X. Wei, HMAS80528; Beijing, 0, I on *M. baccata*, 13 Aug. 1947, col-

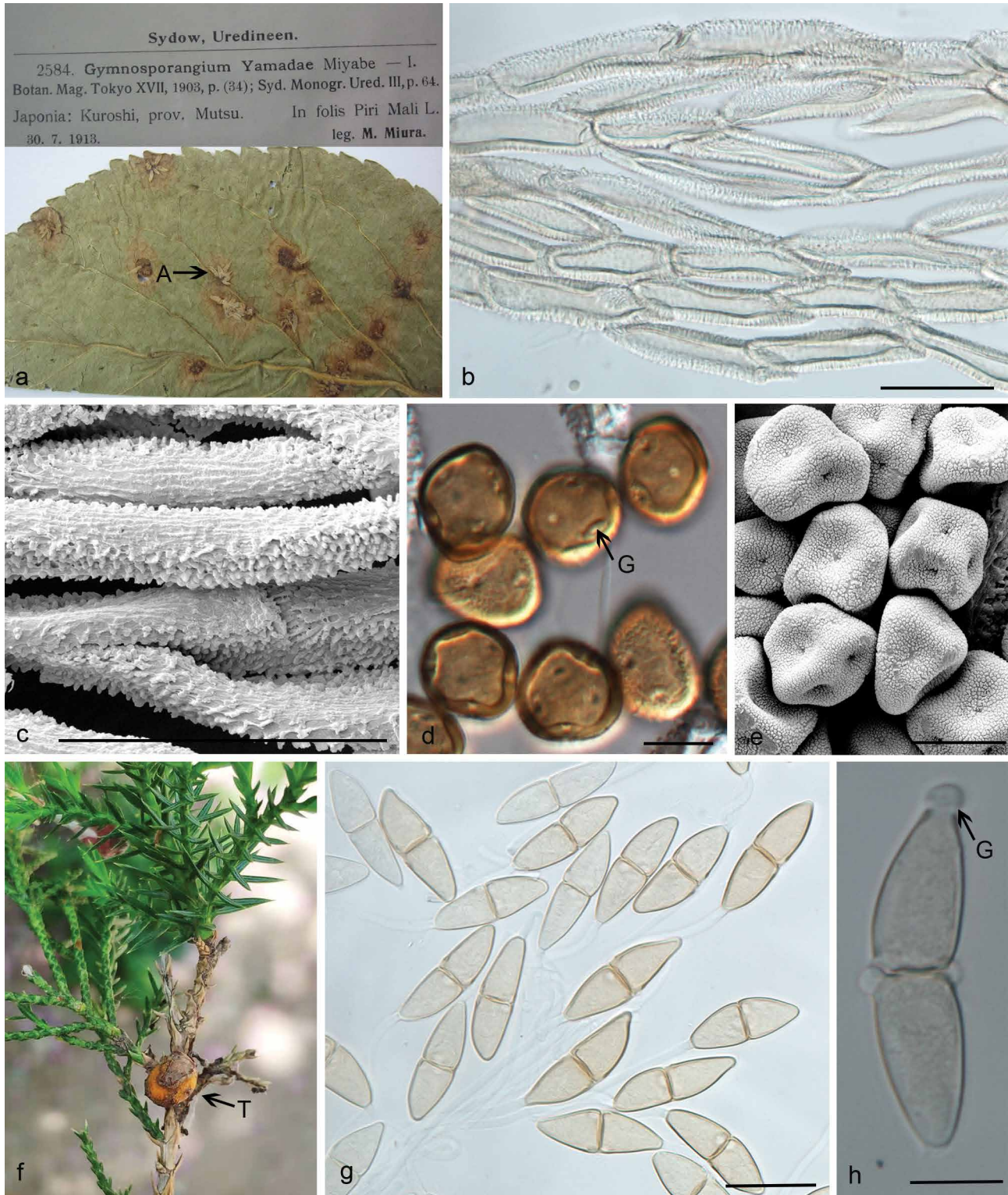


Fig. 15 Morphology of *G. yamadae*. a. Label of type specimen and aecia (A) on the hypophyllous leaf surface; b. linear-rhomboid peridial cells observed by LM; c. ultrastructure of peridial cells observed by SEM; d. globose or ellipsoid aeciospores with scattered germ pores (G) observed by LM; e. ultrastructure of aeciospores observed by SEM; f. foliicolous telia with pulvinate sori; g. 2-celled and pedicellate teliospores with cylindrical and hyaline pedicels; h. 3- or 4-celled teliospores observed by LM. — Scale bars: b–c = 50 µm; d–e, g–h = 20 µm.

lector unknown, HMAS17719 & HMAS17707; Beijing, 0, 1 on *M. baccata*, 19 Sept. 1998, J.Y. Zhuang, HMAS157814, HMAS157815 & HMAS157816; Beijing, 0, 1 on *M. micromalus*, 10 Dec. 2008, J.Y. Zhuang, HMAS243188 & HMAS199333; Beijing, 0, 1 on *Malus* sp., date unknown, Dorsett & Morse, NYBG67267; Beijing, III on *J. chinensis*, Y.C. Wang, HMAS47229; Gansu, Lanzhou, 0, 1 on *M. prunifolia*, 30 June 1974, D. Fu, HMAS36992; Hubei, Shennongjia, 0, 1 on *Malus* sp., L. Guo, HMAS55350 & HMAS55351; Inner Mongolia, Hohhot, III on *J. chinensis*, 15 May 1992, Z.S. Hou, HMAS82779; Jiangsu, Nanjing, 0, 1 on *M. spectabilis*, 7 Sept. 1929, F.L. Tai, HMAS11220; Jiangsu, Wuxi, 0, 1 on *Malus* sp., Q.X. Wu, HMAS14327; Shaanxi, Xian, 0, 1 on *M. mandshurica*, 26 Sept. 1963, Y.C. Wang, HMAS34430; Shanxi, Taiyuan, 0, 1 on *M. prunifolia*, 19 June 1974, B. Li, HMAS36991; Yunnan, Diqing, Shangri-La, 0, 1 on *M. micromalus*, P. Zhao, ZP-R16, ZP-R6001, ZP-R6003 & ZP-R6004. — JAPAN, Iwate prefecture, Mrioka, 0, 1 on *M. communis*, data unknown, K. Togashi, NYBG3009547; Tokyo, 0, 1 on *Malus spectabilis*, 23 June 1994, N. Nambu, NYBG53757; Saitama prefecture, Kamine-mura, 0, 1 on *M. halliana*, 30 June 1931, Y. Shibasaki, NYBG3009548 & NYBG3009550. — USA, New York, 0, 1 on *M. micromalus*, 14 Aug. 1934, G.B. Cummins, CUP-20612.

Host range and geographical distribution confirmed in this study — *Juniperus chinensis* – China, Japan; *Juniperus chinensis* var. *kaizuka* – South Korea; *Malus baccata* – China; *Malus communis* – Japan; *Malus toringo* – South Korea; *Malus mandshurica* – China; *Malus micromalus* – China; *Malus prunifolia* – China; *Malus spectabilis* – China, Japan.

Additional host range and geographical distribution reported in previous studies — *Juniperus chinensis* – USA; *Juniperus chinensis* var. *procumbens* – Japan; *Juniperus chinensis* var. *sargentii* – Japan; *Juniperus sargentii* – Russia; *Juniperus squamata* – Japan; *Malus platycarpa* – Japan; *Malus prunifolia* – Japan; *Malus spontanea* – Japan; *Malus theifera* – Japan; *Malus toringo* – South Korea; *Malus transitoria* – Japan; *Malus yunnanensis* – Japan (Farr & Rossman 2019).

Notes — This species was first reported on *J. chinensis* based on Japanese specimens (Miyabe 1903), but the name was invalid because no description of this species was proposed. One year later, Yamada (1904) described this species in the textbook of plant pathology validating it with a description. Due to lack of holotype specimen, we designated type illustrations of Yamada (1904) as lectotype. In addition, we designated an epitype specimen, which was collected in Japan on

M. domestica in Aomori prefecture in Japan, which is adjacent to type locality. The host alternation of this species between *M. domestica*, *M. spectabilis*, *M. sieboldii* and *J. chinensis* was confirmed by Miyabe (1903). Thereafter, a new name, *G. yamadae* (Miyabe) F. Kern (1911) was used to describe this fungus based on its type specimen on *M. spectabilis*, which was collected by N. Nambu in Tokyo. Due to nomenclatural priority, the name proposed by Kern in 1911 should be abandoned for use, and it was also conspecific to *G. yamadae* Miyabe ex G. Yamada based on our morphological examination of specimens used for species description by Kern. In terms of quarantine, this species is listed as a quarantine pest in North America due to the severe damage it causes on commercial *Malus* and *Pyrus* species (EPPO/CABI 1996a). We confirmed species delineation, host alternation and geographic distribution, which are of vital importance to plant quarantine.

ADDITIONAL TAXONOMIC NOVELTY RECOGNIZED IN THIS STUDY

Gymnosporangium kanas P. Zhao & L. Cai, sp. nov. — MycoBank MB831270; Fig. 16

Etymology. Epithet refers to Kanas Lake, where the type specimen was collected.

Typus. CHINA, Xinjiang, Altay Prefecture, Kanas Lake, aecial stage on *Cotoneaster dammeri*, 16 Aug. 2016, P. Zhao (holotype HMAS248105), SSU, ITS and LSU sequences GenBank MK488124, MK518825 and MK518469.

Spermogonia Group (type 4), foliicolous, epiphyllous, subepidermal, determinate, black or dark brown, 0.1–0.4 mm, with strongly concave hymenia, bounding structures with well-developed periphyses. *Aecia* *Roestelia*-type, fructicolous, roestelioid, white finger-like tubes develop all over fruit, 4–7 mm high, tubular, rupturing at apex; peridium cylindrical, retaining more or less tubular shape, erect or spreading, peridial cells verrucose-rogose, 39–91 µm long, 19–27 µm wide, aeciospores globoid

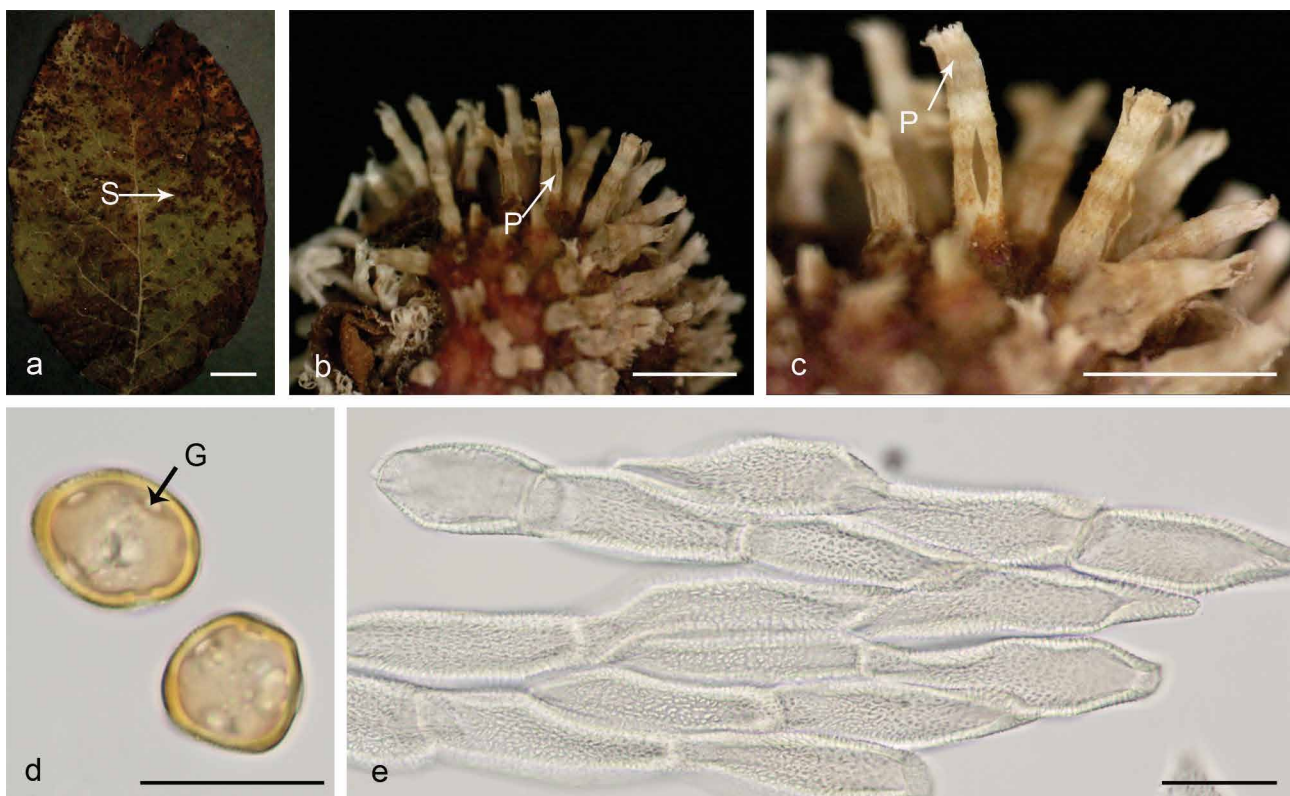


Fig. 16 Morphology of *G. kanas*. a. Spermogonia (S) on the epiphyllous leaf surface; b. aecia only found on fruits; c. peridia cells (P) on fruits; d. globoid or ellipsoid urediniospores observed by light microscope, germ pores (G) scattered; e. peridial cells cylindrical, retaining more or less tubular shape, verrucose-rogose. — Scale bars: a–c = 0.5 mm; d–e = 20 µm.

or broadly ellipsoid, 20–28 × 16–22 µm, verrucose, walls 1.5–3 µm thick. *Uredinia* and *telia* not found.

Additional material examined. CHINA, Xinjiang, Altay Prefecture, Kanas Lake, aecial stage on *Cotoneaster dammeri*, 16 Aug. 2016, P. Zhao, ZP-R481.

KEY TO GYMNASPORANGIUM SPECIES RECOGNIZED IN THIS STUDY

1. Aecia with balanoid peridium, peridial cells oblong, aeciospores relatively small, 15–29 × 14–24 µm, walls large coronate. *G. lachrymiforme*
1. Aecia with tubular peridium 2
2. Peridial cells prismatic, 43–96 × 27–64 µm, rugose with set ridges, peridium cornuted, aeciospores verrucose *G. fenzelianum*
2. Peridial cells rhomboid or oblong 3
3. Peridial cells inner walls densely verrucose with long papillae, aeciospores walls large coronate, basal parts columnar and upper parts separated into several long protuberances *G. spinulosum*
3. Peridial cells inner walls with small papillae 4
4. Aeciospores echinulate 5
4. Aeciospores not echinulate 6
5. Peridial cells inner walls tuberculate, teliospores 2-celled, pedicels carotiform, 10–24 µm diam *G. clavipes*
5. Peridial cells inner walls rugose, teliospores 2-celled, pedicels cylindrical, less than 2.5–3.5 µm diam *G. tremelloides*
6. Peridial cells inner walls and side walls evenly echinulate, 77–148 × 15–29 µm, aeciospores large coronate, teliospores 46–97 × 15–21 µm, pedicels cylindrical, 3.0–7.5 µm diam *G. clavariiforme*
6. Peridial cells inner walls and side walls not echinulate 7
7. Aeciospores verrucose 8
7. Aeciospores coronate 12
8. Aeciospores verrucose with refractive granules, peridial cells inner walls verrucose, teliospores 2–5-celled, pedicels cylindrical, up to 20 µm diam *G. libocedri*
8. Aeciospores verrucose without refractive granules 9
9. Aeciospores large verrucose with large processes, peridial cells densely verrucose, teliospores 1–3-celled *G. miyabei*
9. Aeciospores densely verrucose. 10
10. Peridial cells inner walls densely rugose with elongate small papillae, telia on globoid galls up to 28 mm diam, teliospores 2-celled, 38–69 × 20–33 µm, pedicel cylindrical, hyaline, 5.0–9.5 µm diam *G. nelsonii*
10. Peridial cells inner walls densely rugose without elongate small papillae. 11
11. Peridium cylindrical, lacerate along sides, telia cauliculous, brush-like witches' broom or birds' nests, teliospores 1–4-celled *G. nidus-avis*
11. Peridium cylindrical, rupturing at apex *G. kanas*
12. Peridial cells inner walls and side walls moderately rugose, aeciospores 18–34 × 14–22 µm, telia globoid or reniform galls, 10–40 mm diam, teliospores 2-celled, 35–66 × 16–23 µm *G. juniperi-virginianae*
12. Peridial cells side walls rugose, inner walls small papillae with irregular verruculose with ridge-like papillae 13
13. Aeciospores small coronate, processes 0.3–0.6 µm in height 14
13. Aeciospores large coronate, processes over 1 µm in height 16

14. Peridial cells oblong to rhomboid, telia cauliculous, forming irregularly fusiform swellings of smaller branches, teliospores 2–3-celled *G. monticola*
14. Peridial cells linear-rhomboid, teliospores 2-celled 15
15. Peridium tubular, peridial cells 55–103 × 18–31 µm, telia developing on witches' broom, aggregated bluntly conical, hemispherical, pulvinate or somewhat wedge-shaped *G. cornutum*
15. Peridium cornuted, rupturing in a lace-like network along the sides, telia on globose swellings or small galls up to 9 mm diam *G. yamadae*
16. Peridium cornuted, tardily dehiscent by side lacerations, causing hypertrophy, telia globoid galls up to 12 mm diam *G. corniculans*
16. Peridial cells rhomboid-oblong 17
16. Peridial cells linear-rhomboid 18
17. Peridia minute, up to 2 mm in height, peridial cells relatively large, 69–105 × 33–51 µm, aeciospores large, 27–49 × 24–37 µm *G. shennongjiaense*
17. Peridia up to 8.5 mm in height, peridial cells small, 34–77 × 17–32 µm, aeciospores small, 16–24 × 14–20 µm *G. tiankengense*
18. Peridia up to 7 mm in height, aeciospores small, 18–26 × 14–22 µm, telia developing on witches' broom, hemispherical, pulvinate or somewhat wedge-shaped, teliospores small, 31–50 × 16–27 µm *G. asiaticum*
18. Peridia minute, up to 2 mm in height, aeciospores large, 27–49 × 24–37 µm, telia cauliculous on fusiform or gall-like swellings, teliospores large, 32–85 × 23–32 µm *G. globosum*

DISCUSSION

Differentiation of Gymnosporangium from other rust genera

Since the establishment of the genus *Gymnosporangium* based on rust collections on juniper hosts in Europe, this genus has long been classified in the family *Pucciniaceae* due to its pedicellate teliospores and Group V spermogonia (Hiratsuka & Hiratsuka 1980, Hiratsuka et al. 1992, Cummins & Hiratsuka 2003). However, recent phylogenetic studies suggested its phylogenetic distinction from core *Pucciniaceae* (*Puccinia/Uromyces*) (Maier et al. 2003, Aime 2006, Aime et al. 2018). Here we included representative taxa from the order *Pucciniales* to determine the phylogenetic relationship of *Gymnosporangium* species to other rust genera, especially those in the family *Pucciniaceae*. More than 77 genera from 14 families in the *Pucciniales* were involved, and until now, this phylogeny provides the highest coverage of genera within this order. We confirmed the monophyly of the genus *Gymnosporangium*, and being distinct from other genera in the family *Pucciniaceae*. Morphologically, *Gymnosporangium* produces teliospores with gelatinous pedicels and *Roestelia*-type aecia, which clearly differ from other genera in *Pucciniaceae* (Sydow & Sydow 1915, Arthur 1934, Kern 1973, Cummins & Hiratsuka 2003). In addition, the life cycle of the genus *Gymnosporangium* is unique, having a telial stage on gymnosperms and aecial stage on angiosperms, and such host alternation is different from most rusts on gymnosperms, which have aecial stages on gymnosperms but uredinal/telial stages on angiosperms (Cummins & Hiratsuka 2003). Phylogenetic results also supported morphological distinctions. Thus, we proposed a new family, *Gymnosporangiaceae* to accommodate the genus *Gymnosporangium*. Our phylogenetic results of the order *Pucciniales* further emphasized the need for a taxonomic revision of rust fungi at family level, and the taxonomic criteria (mainly the structure of spermogonia and morphology of teliospores) used by Cummins & Hiratsuka

(1983) were shown to be inappropriate at family level. Further comparative studies need to be conducted to resolve the confusion surrounding the circumscription of families and genera within the *Pucciniales*.

Taxonomic importance of rust fungi using holomorphic morphology

Hitherto approximately 64 *Gymnosporangium* species and 14 species of its asexual morph *Roestelia* have been reported (Kern 1973, Lee & Kakishima 1999a, b, Shen et al. 2018). Most of the reported *Gymnosporangium* species lack an uredinal stage in their life cycles, and both aecial and telial host ranges have long been proven to be ineffective for species recognition (Kern 1973, Hiratsuka et al. 1992, Zhao et al. 2016). Thus, morphological characteristics in aecial structures, i.e., type of aecia, surface ornamentation of peridial cells, and shape, size and colour of aeciospores, served as important taxonomic criteria at species level (Sydow & Sydow 1915, Lee & Kakishima 1999a, b). Previously, aecia within this genus were divided into two types, roestelioid and aecidioid, and roestelioid aecia were further divided into five types based on shape and type of rupture (Parmelee 1965, Kern 1973). Furthermore, 12 types of surface structures in aeciospores and 10 types of peridial cell walls were further recognized among *Gymnosporangium* species (Lee & Kakishima 1999a, b). Our phylogenetic studies support the effectiveness of above-mentioned characters for species recognition. However, these characters alone were still insufficient for species recognition, and the morphology of the telial stage, i.e., septation of teliospores, morphology of pedicel cells and shape of telia, are essential for identification. With the aid of molecular information, the connection of aecia and telia provided additional morphological characters for species recognition, especially for those that shared similar morphologies in certain spore stages. In addition, the lack of life cycle information sometimes led to confusion, such as *G. asiaticum* and its synonyms *G. chinense*, *G. haraeianum*, *G. koreanse*, *G. spiniferum* and *G. unicornis*. Due to the lack of life cycle information, they were proposed as distinct species based on slight differences in teliospore morphology (Sydow & Sydow 1915, Yun et al. 2009). Here we confirmed the host alternation of *G. asiaticum*, and further confirmed these above-mentioned species as conspecific to *G. asiaticum*. Thus, morphological characteristics in the whole life cycle are of vital importance to facilitate accurate species delimitation.

The complexity of host specificity in *Gymnosporangium* species on *Malus*

Our studies further emphasised no clear host specificity among *Gymnosporangium* species in both aecial and telial stages. At plant generic level, most of these *Gymnosporangium* species have their aecial stage on two or more genera within *Rosaceae*, and some species, such as *G. clavariiforme*, can parasitize plants in up to 13 genera in *Rosaceae* (Crowell 1940, Novick 2008). At species level, many *Gymnosporangium* species shared the same telial or aecial hosts and no host specificity was found. In the telial stage, *J. communis* was confirmed as telial host for five *Gymnosporangium* species, i.e., *G. clavariiforme*, *G. cornutum*, *G. gaeumannii*, *G. gracile* and *G. tremelloides*. A similarly situation was found on *J. chinensis*, *J. oxycedrus*, *J. przewalskii* and *J. virginiana*, where they served as hosts of two or even more *Gymnosporangium* species. Similarly, in the aecial stage, *M. domestica*, *M. pumila* and *M. spectabilis* were found to be hosts of two or more *Gymnosporangium* species. Such an overlap in hosts might be caused by complicated evolutionary processes of speciation within the genus. In our previous studies, we found host switches, duplication, losses and failure to diverge all played certain roles in driving speciation in *Gymnosporangium* (Zhao et al. 2016). Thus, multiple

speciation mechanisms exist within the genus which might force the phenomena of overlapping host ranges in both aecial and telial stages.

Contributions of taxonomic studies to plant protection and quarantine

Within the genus *Gymnosporangium*, several species are listed as important quarantine pests worldwide due to their potential threats to commercial fruit cultivars. In the European Union, *G. clavipes*, *G. globosum*, *G. juniperi-virginianae* and *G. yamadadae* are listed in the EPPO A1 list, and *G. asiaticum* is listed in the A2 list (EPPO 2018). In Asia, *G. clavipes*, *G. fuscum*, *G. globosum* and *G. juniperi-virginianae* are treated as quarantine pests in China, Japan, South Korea and adjacent regions (Duan et al. 2017). In North America, *G. fuscum* and *G. yamadadae* are listed as quarantine pests in the USA and Canada (<https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/rppl/rppl-table>). Currently, detection of these quarantine pests relies mainly on morphological characteristics worldwide (EPPO 2017, 2018). However, complexity of host alternation and diverse forms of structures in aecial and telial stages render correct identification impossible, and thus successful interception of these pests in quarantine departments of many countries remains problematic (Duan et al. 2017). In this study we focused on *Gymnosporangium* species infecting commercial apple cultivars and their relatives, and conducted molecular and morphological studies on these above-mentioned quarantine pests. Typification studies were conducted on *G. asiaticum*, *G. fenzelianum*, *G. juniperi-virginianae*, *G. libocedri*, *G. nelsonii*, *G. nidus-avis* and *G. yamadadae*, and morphological data in both aecial and telial stages and DNA sequences were generated, especially from type materials. In addition, host alternation of each species was verified. All these data can be effective for both morphological and molecular detection of those quarantine pests. In addition, comparison of sequence variation of rDNA SSU, ITS and LSU among *Gymnosporangium* species revealed that concatenated data of ITS and LSU obtained a better resolution at the species level, and therefore we recommend this locus as effective barcode for *Gymnosporangium* species.

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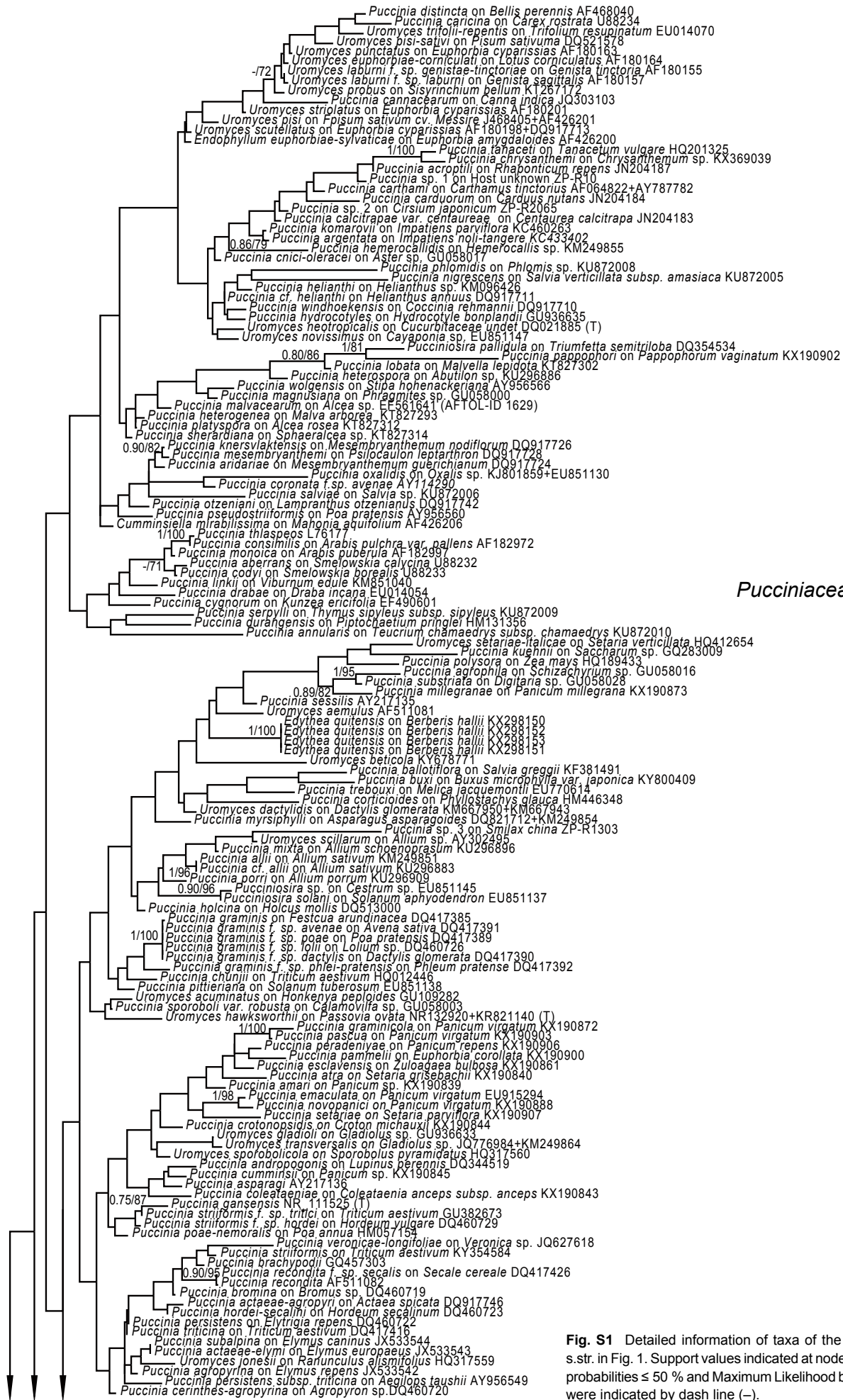
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Supplementary material

Fig. S1 Detailed information of taxa of the family *Pucciniaceae* s.str. in Fig. 1. Support values indicated at nodes. Bayesian posterior probabilities $\leq 50\%$ and Maximum Likelihood bootstrap (ML) $\leq 50\%$ were indicated by dash line (–).

Table S1 rDNA sequence data from selected genera in the *Pucciniales* used for phylogenetic studies.

Table S2 A list of species, specimens and GenBank accession numbers of sequences used for phylogenetic studies at species level.



Pucciniaceae s.str.

Fig. S1 Detailed information of taxa of the family *Pucciniaceae* s.str. in Fig. 1. Support values indicated at nodes. Bayesian posterior probabilities $\leq 50\%$ and Maximum Likelihood bootstrap (ML) $\leq 50\%$ were indicated by dash line (-).

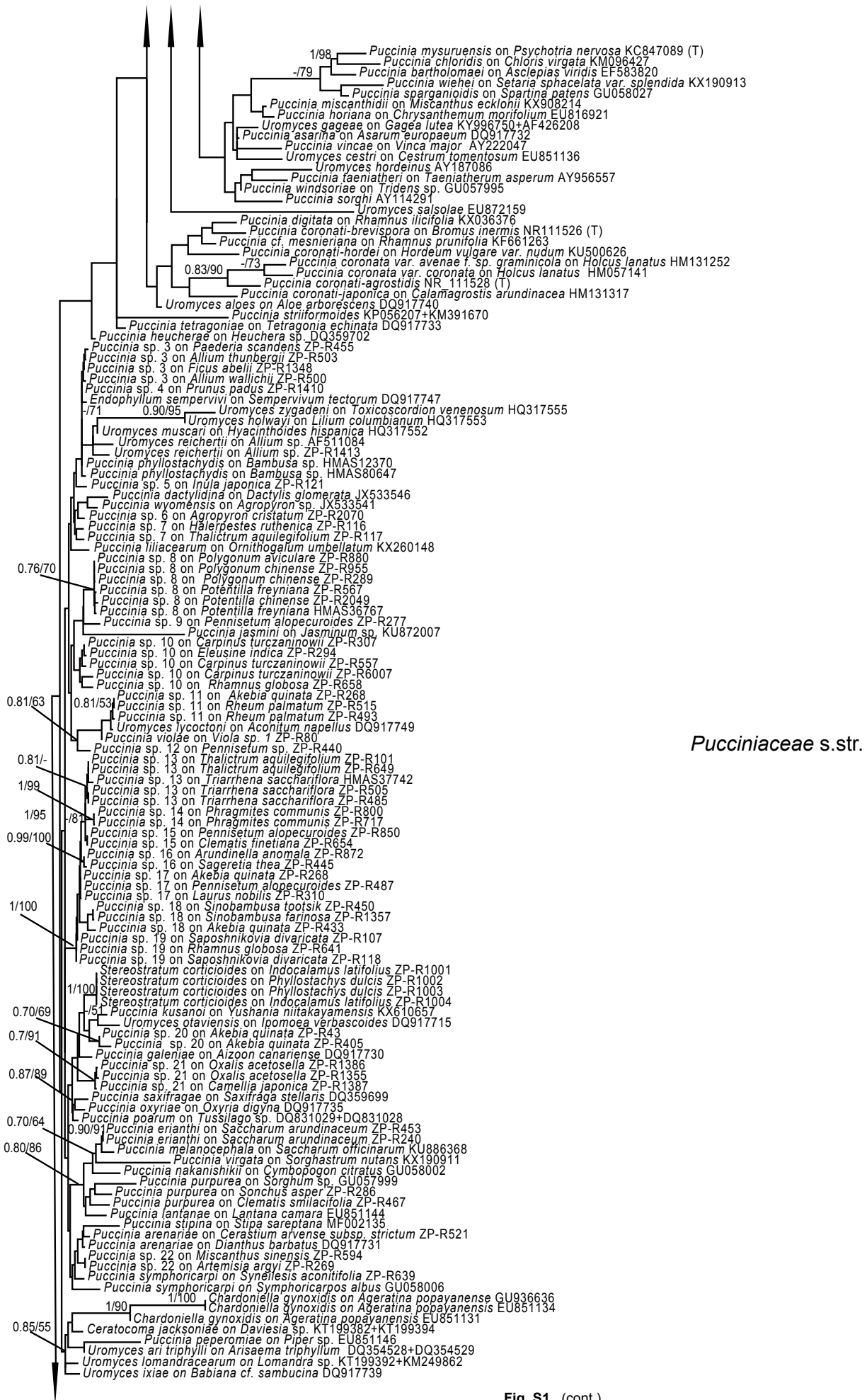


Fig. S1 (cont.)

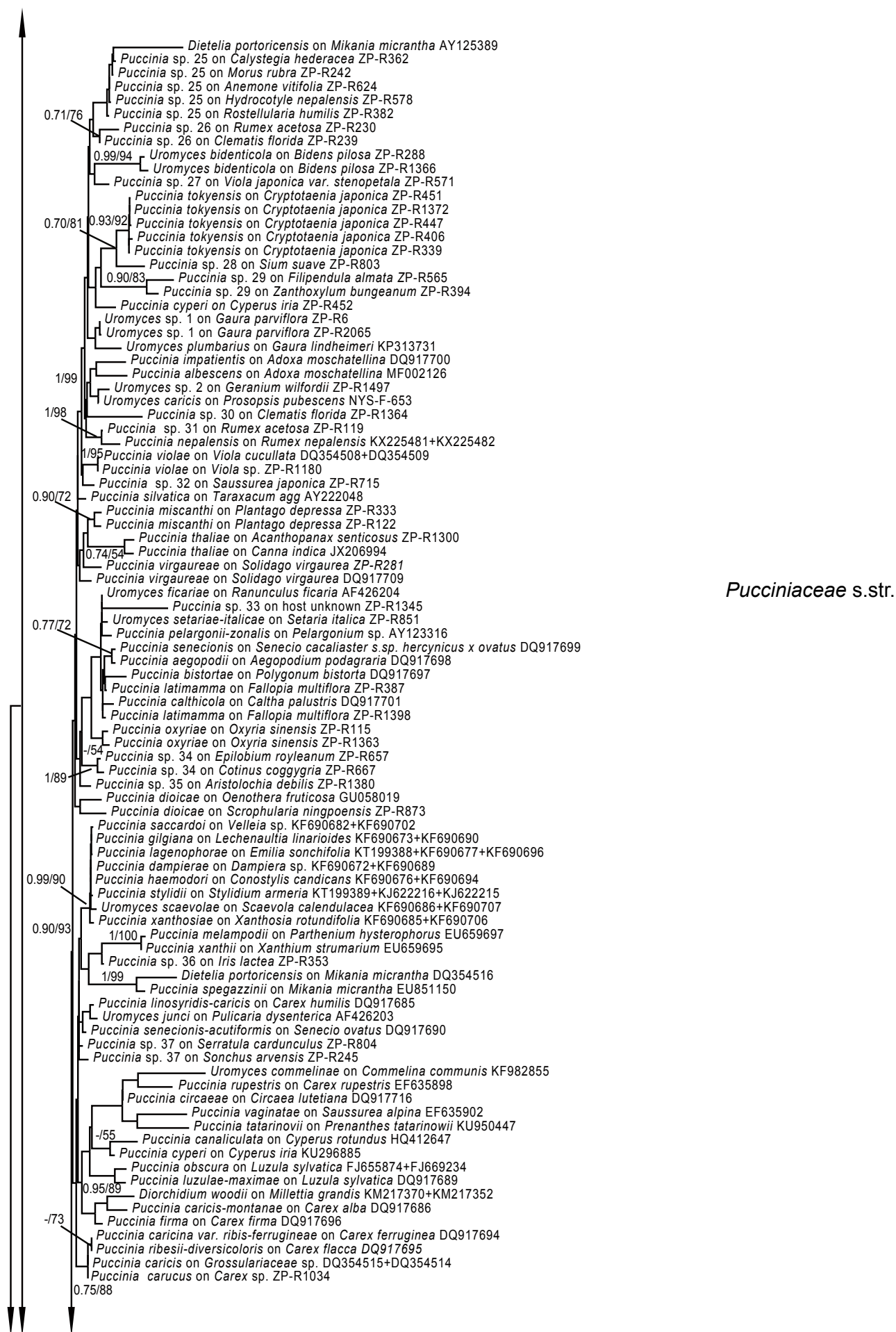


Fig. S1 (cont.)

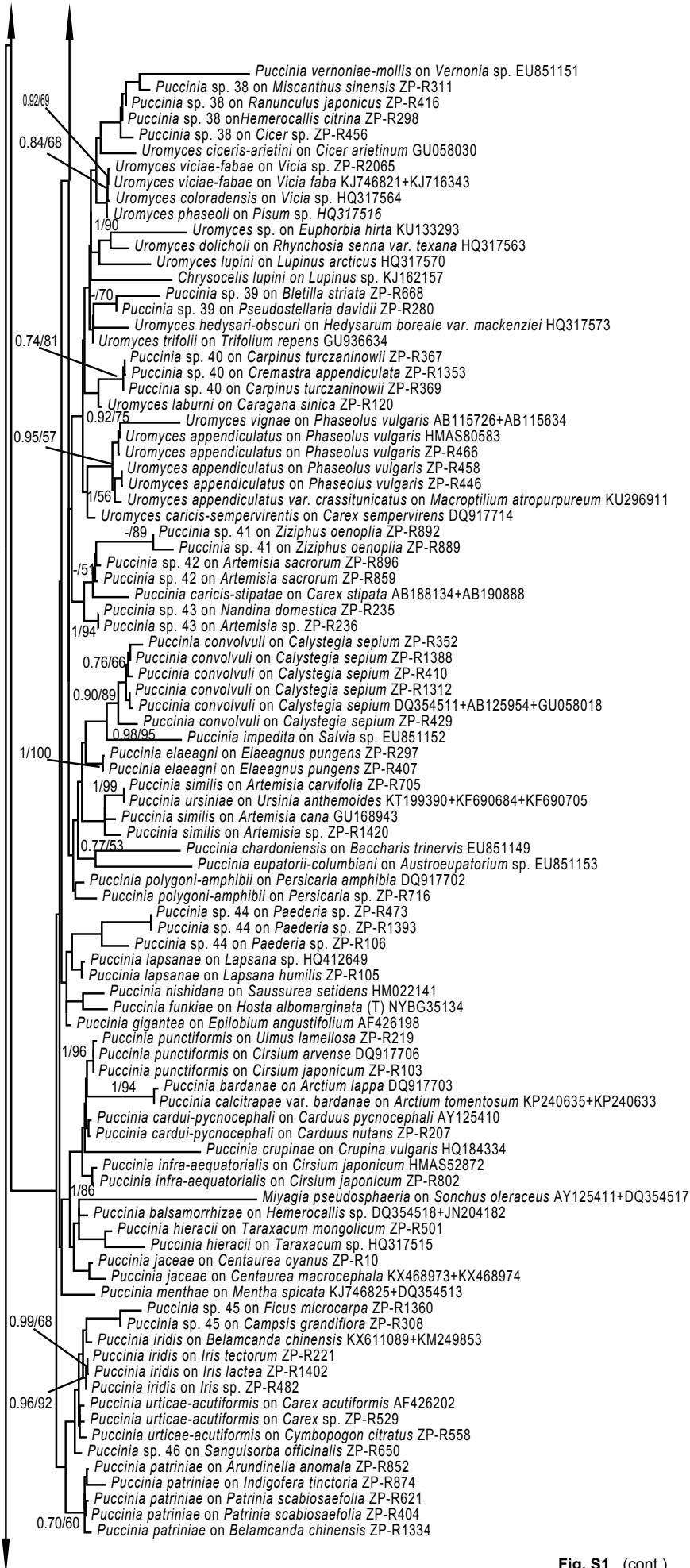
*Pucciniaceae* s.str.

Fig. S1 (cont.)

Table S1 rDNA sequence data from selected genera in the *Pucciniales* used for phylogenetic studies.

Genera	Taxa	References
<i>Achrotelium</i>	1	McTaggart et al. (2016).
<i>Aecidium</i>	2	–*
<i>Allodus</i>	1	Aime (2006), Minnis et al. (2012).
<i>Anthomyces</i>	1	–
<i>Atelocauda</i>	1	Wingfield et al. (2004).
<i>Batistopsora</i>	2	Aime (2006), Beenken (2014).
<i>Blastospora</i>	1	Aime (2006).
<i>Caeoma</i>	2	Wingfield et al. (2004), Crane et al. (2005).
<i>Ceratocoma</i>	1	McTaggart et al. (2016).
<i>Cerotelium</i>	1	Maier et al. (2015).
<i>Chardonella</i>	1	Zuluaga et al. (2011).
<i>Chrysocelis</i>	2	Zuluaga et al. (2011).
<i>Chrysocyclus</i>	1	Zuluaga et al. (2011).
<i>Chrysomyxa</i>	16	Aime (2006), Feau et al. (2011), Padamsee & McKenzie (2014), Cao et al. (2017b).
<i>Coleosporium</i>	10	Sjamsuridzal et al. (1999), Wingfield et al. (2004), Su et al. (2012), Yang et al. (2014).
<i>Cronartium</i>	3	Vogler & Bruns (1998), Aime (2006), Liu et al. (2015).
<i>Cumminsia</i>	1	Maier et al. (2003), Aime (2006).
<i>Cystospora</i>	1	McTaggart et al. (2016).
<i>Dasturella</i>	1	Wingfield et al. (2004).
<i>Dasyospora</i>	11	Beenken et al. (2012).
<i>Desmella</i>	1	McTaggart et al. (2014).
<i>Diaphanopellis</i>	1	Cao et al. (2017b).
<i>Dietelia</i>	2	Wingfield et al. (2004), Aime (2006).
<i>Diorchidium</i>	2	Beenken et al. (2012), Beenken & Wood (2015).
<i>Edythea</i>	1	–
<i>Endocronartium</i>	1	Vogler & Bruns (1998).
<i>Endophyllum</i>	5	Wood & Crous (2005), Maier et al. (2007).
<i>Endoraecium</i>	6	McTaggart et al. (2015).
<i>Gerwasia</i>	1	Wingfield et al. (2004), McTaggart et al. (2014).
<i>Gymnoconia</i>	1	Wingfield et al. (2004), Yun et al. (2011), AFTOL-ID 1630.
<i>Gymnosporangium</i>	21	Novick (2008), Zhao et al. (2016).
<i>Hamaspora</i>	1	McTaggart et al. (2015).
<i>Hemileia</i>	4	Wingfield et al. (2004), Aime (2006), McTaggart et al. (2015).
<i>Hyalospora</i>	2	Sjamsuridzal et al. (1999), Maier et al. (2003), Wingfield et al. (2004), Padamsee & McKenzie (2014).
<i>Kernkampella</i>	1	McTaggart et al. (2015).
<i>Kuehneola</i>	1	Shands et al. (2018), AFTOL-ID 987.
<i>Kweilingia</i>	1	Blomquist et al. (2009).
<i>Leucotelium</i>	2	–
<i>Macruropyxis</i>	3	Beenken & Wood (2015), Martin et al. (2017).
<i>Marvalia</i>	2	Zuluaga et al. (2011), McTaggart et al. (2016).
<i>Masseella</i>	1	Liberato et al. (2014).
<i>Melampsora</i>	31	Tian et al. (2004), Vialle et al. (2013), Zhao et al. (2015), Zhao et al. (2017).
<i>Melampsorella</i>	1	Maier et al. (2003), Wingfield et al. (2004).
<i>Melampsoridium</i>	2	Maier et al. (2003), Wingfield et al. (2004), McKenzie et al. (2013).
<i>Mikronegeria</i>	2	Aime (2006), Padamsee & McKenzie (2014).
<i>Milesina</i>	1	Wingfield et al. (2004), McTaggart et al. (2014).
<i>Miyagia</i>	1	Wingfield et al. (2004), Aime (2006).
<i>Nachidemycus</i>	1	Aime (2006), Padamsee & McKenzie (2014).
<i>Nyssospora</i>	3	Wingfield et al. (2004), Swann & Taylor (1995).
<i>Ochropsora</i>	2	Sjamsuridzal et al. (1999).
<i>Olivea</i>	1	Aime (2006).
<i>Phakopsora</i>	13	Aime (2006), Chatasiri & Ono (2008), Zuluaga et al. (2011), Maier et al. (2015), Pota et al. (2015).
<i>Phragmidium</i>	10	Wingfield et al. (2004), Deadman et al. (2011), McTaggart et al. (2016), Ali et al. (2017).
<i>Physopella</i>	2	Sjamsuridzal et al. (1999), Wingfield et al. (2004).
<i>Pileolaria</i>	3	Wingfield et al. (2004), Aime (2006), AFTOL-ID 988.
<i>Porotenus</i>	1	Matheny et al. (2006), Beenken et al. (2012).
<i>Prospodium</i>	3	Pegg et al. (2013), AFTOL-ID 1401.
<i>Puccinia</i>	241	Kropp et al. (1997), Raguso & Roy (1998), Maier et al. (2003), Wingfield et al. (2004), Engkhaninun et al. (2005), Aime (2006), Szabo (2006), Maier et al. (2007), Langrella et al. (2008), Zale et al. (2008), Alaei et al. (2009), Pedley (2009), Seier et al. (2009), Dixon et al. (2010), Jin et al. (2010), Sampangi et al. (2010), Deadman et al. (2011), Scholler et al. (2011), Zuluaga et al. (2011), Bruckart et al. (2012), Liu & Hambleton (2012), Padamsee & McKenzie (2012), Liu & Hambleton (2013), Liu et al. (2013), Blomquist et al. (2014), Tan et al. (2014), Padamsee & McKenzie (2014), Demers et al. (2015), Liu et al. (2015), Mulvey & Hambleton (2015), Kabaktepe et al. (2016), Mahadevakumar et al. (2016), McTaggart et al. (2016), Demers et al. (2017), Shen & Huang (2017), AFTOL-ID 1629.
<i>Pucciniastrum</i>	8	Wingfield et al. (2004), Liang et al. (2006), Padamsee & McKenzie (2014).
<i>Puccinosira</i>	3	Aime (2006), Zuluaga et al. (2011).
<i>Puccorchidium</i>	1	Beenken & Wood (2015).
<i>Racospermyces</i>	1	Wingfield et al. (2004), Scholler & Aime (2006), Liu et al. (2015).
<i>Ravenelia</i>	5	Aime (2006).
<i>Roestelia</i>	3	Novick (2008).
<i>Sphaerophragmium</i>	1	McTaggart et al. (2015).
<i>Sphenorchidium</i>	1	Beenken & Wood (2015).
<i>Sphenospora</i>	3	Aime (2006), Beenken & Wood (2015).
<i>Thekopsora</i>	4	McTaggart et al. (2016), Yang et al. (2014), Yang et al. (2015).
<i>Trachyspora</i>	1	Maier et al. (2003), Aime (2006).
<i>Tranzschelia</i>	5	Deadman et al. (2007), Blomquist et al. (2015).
<i>Triphragmium</i>	1	Maier et al. (2003), Wingfield et al. (2004), Yun et al. (2011).
<i>Uredinopsis</i>	2	Sjamsuridzal et al. (1999), Wingfield et al. (2004), McTaggart et al. (2014).
<i>Uredo</i>	4	Hernandez et al. (2005), McTaggart et al. (2016).
<i>Uromyces</i>	57	Pfunder et al. (2001), Maier et al. (2003), Anikster et al. (2004), Wingfield et al. (2004), Aime (2006), Dixon et al. (2010), Yun et al. (2010), Zuluaga et al. (2011), Liu et al. (2015), Souza et al. (2015), McTaggart et al. (2016), AFTOL-ID 976.
<i>Uromycladium</i>	4	McTaggart et al. (2015).

Table S2 List of species, specimens and GenBank accession numbers of sequences used for phylogenetic studies at species level.

Species	Specimen No. ^a	Host	Spore stage	GenBank Accession No. ^b			References
				SSU	ITS	LSU	
<i>Gymnosporangium amelanchieris</i>	20141009	<i>Amelanchier ovalis</i>	0,1	—	KP261040	KP261041	Fernández & Alvarado (2016)
	20140331-1	<i>Juniperus oxycedrus</i>	III	—	KIM486541	KIM486546	Fernández & Alvarado (2016)
<i>G. asiaticum</i>	HMAS135599	<i>Cupressus duclouxia</i>	III	MN604940	MN605664	MN605742	This study
	CUP-0016	<i>Juniperus chinensis</i>	III	MN642598	MN642593	MN642617	This study
	HMAS11935	<i>Juniperus chinensis</i>	III	MN604941	MN605665	MN605743	This study
	HMAS165302	<i>Juniperus chinensis</i>	III	MN604942	MN605666	MN605744	This study
	HMAS172366	<i>Juniperus chinensis</i>	III	MN604943	KU288703	KU342779	This study
	HMAS2503	<i>Juniperus chinensis</i>	III	MN604944	MN605667	MN605745	This study
	HMAS47228	<i>Juniperus chinensis</i>	III	MN604945	KU342736	KU342774	This study
	HMAS47229	<i>Juniperus chinensis</i>	III	MN604946	KU288643	KU342776	This study
	HMAS47728	<i>Juniperus chinensis</i>	III	MN604947	MN605668	MN605746	This study
	HMAS165301	<i>Juniperus chinensis</i>	III	MN604973	KU288658	KU342771	This study
	HMAS37835	<i>Juniperus tibetica</i>	III	MN604974	—	—	This study
	IBA5704	<i>Juniperus chinensis</i>	III	KJ72016 ^{1b}	—	—	Novick (2008)
	F0027941	<i>Juniperus chinensis</i>	III	KP308392 ^b	—	—	Shen et al. (2018)
	BJFC-R01834	<i>Juniperus chinensis</i>	III	—	KR814568	KT719165	Cao et al. (2016)
	BJFC-R01835	<i>Juniperus chinensis</i>	III	—	KR814569	KT719166	Cao et al. (2016)
	TNM F0029761	<i>Juniperus chinensis</i>	III	KX355281 ^b	—	—	Shen et al. (2018)
	TNM F0029762	<i>Juniperus chinensis</i>	III	KX355282 ^b	—	—	Shen et al. (2018)
	TNM F0029763	<i>Juniperus chinensis</i>	III	KX355284 ^b	—	—	Shen et al. (2018)
	TNM F0029764	<i>Juniperus chinensis</i>	III	KX355285 ^b	—	—	Shen et al. (2018)
	TNM F0029765	<i>Juniperus chinensis</i>	III	KX355286 ^b	—	—	Shen et al. (2018)
	TNM F0030602	<i>Juniperus chinensis</i>	III	KY964736 ^b	—	—	Shen et al. (2018)
	TNM F0030603	<i>Juniperus chinensis</i>	III	KY964737 ^b	—	—	Shen et al. (2018)
	TNM F0030601	<i>Juniperus chinensis</i>	III	KY964753 ^b	—	—	Shen et al. (2018)
	NTJ F100002	<i>Juniperus chinensis</i>	III	KY964754 ^b	—	—	Shen et al. (2018)
	HKRF12073	<i>Juniperus chinensis</i>	III	—	—	EF990780	Yun et al. (2009)
	HKRF11974	<i>Juniperus chinensis</i> cv. <i>kaizuka</i>	III	—	—	FJ848741	Yun et al. (2009)
	HKRF11977	<i>Juniperus chinensis</i> cv. <i>kaizuka</i>	III	—	—	FJ848744	Yun et al. (2009)
HKRF12074	<i>Juniperus chinensis</i> cv. <i>kaizuka</i>	III	—	—	FJ848750	Yun et al. (2009)	
HKRF11971	<i>Juniperus chinensis</i> var. <i>globosa</i>	III	—	—	FJ848767	Yun et al. (2009)	
HKRF11972	<i>Juniperus chinensis</i> var. <i>globosa</i>	III	—	—	FJ848768	Yun et al. (2009)	
HKRF11976	<i>Juniperus chinensis</i> cv. <i>kaizuka</i>	III	—	—	FJ848743	Yun et al. (2009)	
HKRF11978	<i>Juniperus chinensis</i> cv. <i>kaizuka</i>	III	—	—	FJ848745	Yun et al. (2009)	
HKRF11979	<i>Juniperus chinensis</i> cv. <i>kaizuka</i>	III	—	—	FJ848746	Yun et al. (2009)	
HKRF11980	<i>Juniperus chinensis</i> cv. <i>kaizuka</i>	III	—	—	FJ848747	Yun et al. (2009)	
HKRF11975	<i>Juniperus chinensis</i> var. <i>sargentii</i>	III	—	—	FJ848742	Yun et al. (2009)	
HKRF11973	<i>Juniperus chinensis</i> var. <i>sargentii</i>	III	—	—	FJ848769	Yun et al. (2009)	
HMAS45640	<i>Juniperus excelsa</i>	III	MN604948	MN605669	MN605747	This study	
CUP-57311	<i>Malus ioensis</i> var. <i>plena</i>	0,1	MN604949	MN605670	MN605748	This study	
HMAS172325	<i>Malus asiatica</i>	0,1	MN604950	MN605671	MN605749	This study	
HMAS11217	<i>Malus domestica</i>	0,1	MN604951	MN605672	MN605750	This study	
HMAS135289	<i>Malus domestica</i>	0,1	MN604952	KU288657	KU342773	This study	
HMA14328	<i>Malus pumila</i>	0,1	MN604953	KU288661	KU342772	This study	
HMAS135598	<i>Malus pumila</i>	0,1	—	MN605673	MN605751	This study	
HMAS14327	<i>Malus pumila</i>	0,1	—	KU288671	KU342775	This study	
HMAS17719	<i>Malus pumila</i>	0,1	MN604954	MN605674	MN605752	This study	
HMAS26426	<i>Malus pumila</i>	0,1	MN604955	MN605675	MN605753	This study	
HMAS56909	<i>Malus pumila</i>	0,1	MN604956	MN605676	MN605754	This study	
ZP-R1375	<i>Malus pumila</i>	0,1	MK488389	MK518977	MK518675	This study	

Table S2 (cont.)

Species	Specimen No. ^a	Host	Spore stage	GenBank Accession No. ^b			References
				SSU	ITS	LSU	
<i>G. asiaticum</i> (cont.)	ZP-R1376	<i>Malus pumila</i>	0,1	MN604957	MK518987	MK518686	This study
	ZP-R1412	<i>Malus pumila</i>	0,1	MN604958	MN605677	MN605755	This study
	ZP-R201	<i>Malus pumila</i>	0,1	MN604959	MK518959	MK518654	This study
	ZP-R203	<i>Malus pumila</i>	0,1	MK488432	MK518960	MK518655	This study
	ZP-R204	<i>Malus pumila</i>	0,1	MK488480	MK519005	MK518708	This study
	ZP-R205	<i>Malus pumila</i>	0,1	–	MK518866	MK518740	This study
	ZP-R215	<i>Malus pumila</i>	0,1	MK488223	MK518867	MK518531	This study
	ZP-R228	<i>Malus pumila</i>	0,1	MN604961	MN605678	MN605756	This study
	ZP-R301	<i>Malus pumila</i>	0,1	MN604962	MN605679	MN605757	This study
	ZP-R324	<i>Malus pumila</i>	0,1	MN604963	–	MK518712	This study
	ZP-R336	<i>Malus pumila</i>	0,1	MK488175	MN605680	MN605758	This study
	ZP-R422	<i>Malus pumila</i>	0,1	MK488176	MK518845	MK518501	This study
	ZP-R614	<i>Malus pumila</i>	0,1	MK488124	MK518825	MK518469	This study
	ZP-R617	<i>Malus pumila</i>	0,1	MK488162	–	–	This study
	ZP-R773	<i>Malus pumila</i>	0,1	MN604964	MN605681	MN605759	This study
	ZP-R774	<i>Malus pumila</i>	0,1	MN604965	–	–	This study
	ZP-R778	<i>Malus pumila</i>	0,1	MN604966	MN605682	MN605760	This study
	ZP-R779	<i>Malus pumila</i>	0,1	MN604967	MN605683	MN605761	This study
	ZP-R783	<i>Malus pumila</i>	0,1	MK488171	–	–	This study
	ZP-R876	<i>Malus pumila</i>	0,1	MN604968	MN605684	MN605762	This study
	ZP-R960	<i>Malus pumila</i>	0,1	MK488181	MK518849	MK518506	This study
	ZP-R961	<i>Malus pumila</i>	0,1	MN604969	MN605685	MN605763	This study
	ZP-R6021	<i>Malus pumila</i>	0,1	MK488289	MK518911	–	This study
	HMAS38650	<i>Malus pumila</i>	0,1	MN604970	MN605686	MN605764	This study
	HMAS11219	<i>Malus spectabilis</i>	0,1	MN604971	MN605687	MN605765	This study
	HMAS12970	<i>Malus spectabilis</i>	0,1	–	MN605688	MN605766	This study
	HMAS55351	<i>Malus spectabilis</i>	0,1	MN604972	MN605689	MN605767	This study
	CUP-20544	<i>Malus sp.</i>	0,1	MK488173	MK519048	MK518500	This study
	CUP-17524	<i>Malus sp.</i>	0,1	–	MN605690	MN605768	This study
	HMAS24616	<i>Malus sp.</i>	0,1	–	KU288672	KU342766	This study
	NYBG60678	<i>Malus sp.</i>	0,1	MK488214	MK518863	MK518527	This study
	NTU F100003	<i>Pyrus lindleyi</i>	0,1	MF377396 ^a	–	–	Shen et al. (2018)
	TNM F0027942	<i>Pyrus pyrifolia</i>	0,1	KP308393 ^a	–	–	Shen et al. (2018)
TNM F0027943	<i>Pyrus pyrifolia</i>	0,1	KP308394 ^a	–	–	Shen et al. (2018)	
<i>G. clavariiforme</i>	LD 1019	<i>Crataegus orientalis</i>	0,1	HM114220 ^b	–	–	Dervis et al. (2010)
	CUP-2146	<i>Juniperus communis</i>	III	–	KU288679	KU342767	This study
	HMAS67951	<i>Juniperus communis</i>	III	MN604975	KU288644	KU342765	This study
<i>G. clavipes</i>	HMAS24626	<i>Malus communis</i>	0,1	MN604976	KU288672	KU342766	This study
	NYBG461394	<i>Crataegus sp.</i>	0,1	MN604977	MN605691	MN605769	This study
	CPO 18.01	<i>Crataegus sp.</i>	0,1	–	–	KM382067	Dervis et al. (2010)
	NYS-F-775	<i>Juniperus virginiana</i>	III	MK488179	MK518847	MK518583	This study
	CUP-18207	<i>Juniperus virginiana</i>	III	MN604978	MN605692	MN605770	This study
	RN140	<i>Juniperus virginiana</i>	III	KJ720155 ^b	–	–	Novick (2008)
	BPI 871102	<i>Malus domestica</i>	0,1	DQ354546	–	–	Aime et al. (2018)
	CUP-13530	<i>Malus sp.</i>	0,1	MN604979	–	–	This study
	GSU41566	unknown	0,1	U41566	–	–	Swann & Taylor (1995)
	ECS159	unknown	0,1	AY123309	–	–	Wingfield et al. (2004)
	<i>G. confusum</i>	20140808B-H22	<i>Crataegus mongyna</i>	0,1	–	KP261042	KP261043
20180506-M1		<i>Crataegus mongyna</i>	0,1	MH595612 ^b	–	–	Shen et al. (2018)

Table S2 (cont.)

Species	Specimen No. ^a	Host	Spore stage	GenBank Accession No. ^b			References	
				SSU	ITS	LSU		
<i>G. confusum</i> (cont.)	20180513-M6	<i>Crateagus mongyna</i>	0, I	MH595613 ^b			Shen et al. (2018)	
	20180520-M7	<i>Crateagus mongyna</i>	0, I	MH595614 ^b			Shen et al. (2018)	
	20180526-M11	<i>Crateagus mongyna</i>	0, I	MH595615 ^b			Shen et al. (2018)	
	20140330-2	<i>Juniperus oxycedrus</i>	III	—	KP261046	KP261047	Fernández & Alvarado (2016)	
	20150227-M14	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	III	—	KT160257	KT16026	Fernández & Alvarado (2016)	
<i>G. corniculans</i>	CUP-3087	<i>Amelanchier canadensis</i>	0, I	MN604980	MN605693	MN605771	This study	
	BPI 738115	<i>Amelanchier</i> sp.	0, I	KJ720167 ^b			Novick (2008)	
	RUP-19705	<i>Malus domestica</i>	0, I	MN604981	MN605694	MN605772	This study	
	RSP 98-140	<i>Juniperus virginiana</i>	III	KJ720174 ^b			Novick (2008)	
<i>G. corniforme</i>	TNM F0028736	<i>Juniperus formosana</i>	III	KY964741 ^b			Shen et al. (2018)	
	TNM F0028738	<i>Juniperus formosana</i>	III	KY964743 ^b			Shen et al. (2018)	
	TNM F0030469	<i>Sorbus randaletensis</i>	III	KY964751 ^b			Shen et al. (2018)	
	TNM F0029302	<i>Sorbus randaletensis</i>	III	KY964747 ^b			Shen et al. (2018)	
	<i>G. cornutum</i>	PPR0020M2	<i>Juniperus communis</i>	III	—	MG573153	MG573214	Prats & Alvarado (unpubl.)
HKFRI 2105		<i>Juniperus rigida</i>	III	—	—	FJ848766	Yun et al. (2009)	
HMAS12940		<i>Malus spectabilis</i>	0, I	—	KU288667	KU342735	This study	
BPI 910184		<i>Sorbus americana</i>	0, I	KY764066 ^b			Demers et al. (unpubl.)	
PPR1299CM1		<i>Sorbus aucuparia</i>	0, I	—	—	MG573215	Fernández & Alvarado (unpubl.)	
WM 1093		<i>Sorbus aucuparia</i>	0, I	—	—	AF426210	Maier et al. (2003)	
PPR1307CM2		<i>Sorbus aucuparia</i>	0, I	—	MG573154	MG573213	Prats & Alvarado (unpubl.)	
20170926-H1		<i>Sorbus aucuparia</i>	0, I	—	—	MG561881	Prats P. Alvarado P. (unpubl.)	
RN23		<i>Chamaecyparis thyoides</i>	III	KJ720156 ^b			Novick (2008)	
RSP 04-86		<i>Gillenia trifoliata</i>	0, I	KJ720170 ^b			Novick (2008)	
<i>G. fenzelianum</i>		HMAS33357	<i>Malus kansuensis</i>	0, I	—	MN605695	MN605773	This study
		HMAS38649	<i>Malus kansuensis</i>	0, I	—	KU288690	KU342752	This study
	ZP-R14	<i>Malus kansuensis</i>	0, I	—	MN605696	MN605774	This study	
	ZP-R3	<i>Malus kansuensis</i>	0, I	—	MN605697	MN605775	This study	
	RSP80-14	<i>Chamaecyparis thyoides</i>	III	KJ720171 ^b			Novick (2008)	
<i>G. fraternum</i>	BPI118807	<i>Cupressus arizonica</i>	III	KJ720173 ^b			Novick (2008)	
	RSP99-98	<i>Juniperus communis</i>	III	KJ720169 ^b			Novick (2008)	
	<i>G. globosum</i>	ENCB121368	<i>Crateagus mexicana</i>	0, I	—	—	KX137840	Alvarado-Rosales et al. (2015)
ENCB121369		<i>Crateagus mexicana</i>	0, I	—	—	KX137841	Alvarado-Rosales et al. (2015)	
NYBG237085		<i>Juniperus virginiana</i>	III	MN604982	KU288654	KU342713	This study	
CUP-1553		<i>Malus</i> sp.	0, I	MN604983	MN605698	MN605776	This study	
20160606-M2		<i>Amelanchier ovalis</i>	0, I	KY440115 ^b			Fernández & Alvarado (unpubl.)	
<i>G. gracile</i>	20160519	<i>Crateagus monogyna</i>	0, I	KY440114 ^b			Fernández & Alvarado (unpubl.)	
	20140529-1a	<i>Cydonia oblonga</i>	0, I	—	KM486543	KM486545	Fernández & Alvarado (2016)	
	20150417-M1	<i>Juniperus communis</i>	III	KT160260 ^b			Fernández & Alvarado (2016)	
	20140330-2	<i>Juniperus communis</i>	III	—	—	KP261047	Fernández & Alvarado (2016)	
	20120515	<i>Juniperus communis</i>	III	—	—	KP261049	Fernández & Alvarado (unpubl.)	
	HML 841	<i>Juniperus communis</i>	III	—	—	AF426211	Maier et al. (2003)	
	20140326-1	<i>Juniperus oxycedrus</i>	III	—	KM486542	KM486544	Fernández & Alvarado (unpubl.)	
	20150321-1-M1	<i>Juniperus oxycedrus</i>	III	—	KU183500	—	Fernández & Alvarado (2016)	
	BJFC R01984	<i>Juniperus przewalskii</i>	III	—	NR154077	KT719161	Cao et al. (2017a)	
	BJFC R01985	<i>Juniperus przewalskii</i>	III	—	KT719168	KT719162	Cao et al. (2017a)	

Table S2 (cont.)

Species	Specimen No. ^a	Host	Spore stage	GenBank Accession No. ^b			References	
				SSU	ITS	LSU		
<i>G. japonicum</i> 1	HMAS79186	<i>Juniperus chinensis</i>	III	-	KU288669	KU342722	This study	
	HKFR1 1987	<i>Juniperus chinensis</i>	III	-	-	FJ848751	Yun et al. (2009)	
	HKFR1 1988	<i>Juniperus chinensis</i>	III	-	-	FJ848752	Yun et al. (2009)	
	HKFR1 1992	<i>Juniperus chinensis</i>	III	-	-	FJ848755	Yun et al. (2009)	
	HKFR1 1993	<i>Juniperus chinensis</i> var. <i>horizontalis</i>	III	-	-	FJ848756	Yun et al. (2009)	
	HMAS14315	<i>Juniperus</i> sp.	III	-	KU288641	KU342745	This study	
	20170926-H1	<i>Sorbus aucuparia</i>	0,1	-	-	MG572221	Fernández & Alvarado (unpubl.)	
	<i>G. japonicum</i> 2	HKFR1 1997	<i>Juniperus chinensis</i> var. <i>globosa</i>	III	-	-	FJ848759	Yun et al. (2009)
		HKFR1 1995	<i>Juniperus chinensis</i> var. <i>horizontalis</i>	III	-	-	FJ848758	Yun et al. (2009)
		HKFR1 1994	<i>Juniperus chinensis</i> var. <i>sargentii</i>	III	-	-	FJ848757	Yun et al. (2009)
		NYBG461220	<i>Juniperus virginiana</i>	III	MN604984	KU288652	KU342743	This study
		NYBG1391099	<i>Juniperus virginiana</i>	III	MN604985	KU288647	KU342712	This study
	<i>G. juniperi-virginianae</i>	NYBG237070	<i>Juniperus virginiana</i>	III	MN604986	KU288656	KU342718	This study
		NYBG237046	<i>Juniperus virginiana</i>	III	MN604987	KU288655	KU342719	This study
		NYBG23036	<i>Juniperus virginiana</i>	III	MN604988	KU288637	KU342710	This study
HMAS43709		<i>Juniperus virginiana</i>	III	MN604989	-	-	This study	
RSP98-137		<i>Juniperus virginiana</i>	III	KJ720176 ^a	-	-	Novick (2008)	
MCA3585		<i>Juniperus virginiana</i>	III	-	MG917687	MG907217	Fernández & Alvarado (unpubl.)	
PBM2530		<i>Juniperus virginiana</i>	III	-	DQ267127	AY629316	Matheny & Hibbett (unpubl.)	
DAOM 234434		<i>Juniperus virginiana</i>	III	-	HQ317510	-	Liu et al. (2015)	
HMAS2218		<i>Juniperus scopulorum</i>	III	-	-	KU342767	This study	
HMAS6725		<i>Juniperus</i> sp.	III	-	-	KU342736	This study	
TDB1345		<i>Juniperus</i> sp.	III	-	-	AF522167	Wingfield et al. (2004)	
CUP-24472		<i>Malus angustifolia</i>	0,1	MN604990	MN605699	MN605777	This study	
HMAS74424		<i>Malus baccata</i>	0,1	MN642602	MN642597	MN642621	This study	
CUP-24468		<i>Malus coronaria</i>	0,1	MN604991	MN605700	MN605778	This study	
CUP-55712		<i>Malus coronaria</i>	0,1	MN604992	MN605701	MN605779	This study	
CUP-45235	<i>Malus coronaria</i>	0,1	MN604993	MN605702	MN605780	This study		
CUP-24473	<i>Malus coronaria</i>	0,1	MN604994	MN605703	MN605781	This study		
CUP-20257	<i>Malus domestica</i>	0,1	MN604995	KU288678	KU342716	This study		
CUP-17321	<i>Malus domestica</i>	0,1	MN604996	MN605704	MN605782	This study		
CUP-1551	<i>Malus domestica</i>	0,1	MN604997	MN605705	MN605783	This study		
TNM F0029763	<i>Malus domestica</i>	0,1	KY964761 ^b	-	-	Shen et al. (2018)		
CUP-20153	<i>Malus domestica</i>	0,1	MN604999	MN605707	MN605785	This study		
CUP-51030	<i>Malus domestica</i>	0,1	MN605000	MN605708	MN605786	This study		
CUP-731	<i>Malus domestica</i>	0,1	MN605001	MN605709	MN605787	This study		
CUP-21697	<i>Malus domestica</i>	0,1	MN605002	MN605710	MN605788	This study		
CUP-20161	<i>Malus domestica</i>	0,1	MN605003	-	-	This study		
CUP-20164	<i>Malus domestica</i>	0,1	MN605004	MN605711	MN605789	This study		
CUP-19919	<i>Malus domestica</i>	0,1	MN605005	MN605712	MN605790	This study		
CUP-382	<i>Malus domestica</i>	0,1	MN605006	MN605713	MN605791	This study		
CUP-20157	<i>Malus domestica</i>	0,1	MN642601	MN605714	MN605792	This study		
CUP-14	<i>Malus domestica</i>	0,1	MN605006	MN642596	MN642620	This study		
CUP-20165	<i>Malus domestica</i>	0,1	MN605007	KU288677	KU342708	This study		
CUP-24469	<i>Malus domestica</i>	0,1	-	-	-	This study		
CUP-594	<i>Malus glaucescens</i>	0,1	MN605706	MN605784	MN605784	This study		
CUP-595	<i>Malus ioensis</i>	0,1	KU288676	KU342709	KU342709	This study		
CUP-20162	<i>Malus</i> sp.	0,1	MN605715	MN605793	MN605793	This study		

Table S2 (cont.)

Species	Specimen No. ^a	Host	Spore stage	GenBank Accession No. ^b			References
				SSU	ITS	LSU	
<i>G. kanas</i>	HMAS248105	<i>Cotoneaster dammeri</i>	0,1	MK488124	MK518825	MK518469	This study
	ZP-R481	<i>Cotoneaster dammeri</i>	0,1	MK488115	MK518821	MK518463	This study
	ZP-R614	<i>Cotoneaster dammeri</i>	0,1	MK488124	MK518825	MK518469	This study
<i>G. kernianum</i>	RSP05-37	<i>Juniperus utahensis</i>	III	KJ720177 ^a			Novick (2008)
<i>G. lachnymiforme</i>	HMAS248123	<i>Malus</i> sp.	0,1	-	MN605716	MN605794	This study
<i>G. libocedri</i>	U1469	<i>Amelanchier alnifolia</i>	III	-	MG907206	MG907218	Aime et al. (2018)
	HMAS49246	<i>Calocedrus decurrens</i>	III	MN605009	MN605717	MN605795	This study
	HMAS45643	<i>Calocedrus decurrens</i>	III	MN605010	MN605718	MN605796	This study
	TDB1519	<i>Calocedrus decurrens</i>	III	AY123290	AF522168	-	Wingfield et al. (2004)
	IBA 6650	<i>Chamaecyparis pisifera</i>	III	KJ720178 ^b			Novick (2008)
<i>G. miyabei</i>	DAOM186133	<i>Juniperus communis</i>	III	KJ720185 ^b			Novick (2008)
	CUP-56165	<i>Malus sylvestris</i>	0,1	-	KU288675	KU342748	This study
<i>G. monticola</i>	HKFR1 1983	<i>Juniperus rigida</i>	III	-		FJ848770	Yun et al. (2009)
	RN152	<i>Juniperus rigida</i>	III	KJ720168 ^a			Novick (2008)
	HKFR1 1985	<i>Juniperus rigida</i>	III	-		FJ848771	Yun et al. (2009)
	HMAS44394	<i>Malus pumila</i>	0,1	-	KU288683	KU342754	This study
	HMAS44514	<i>Malus pumila</i>	0,1	-	KU288696	KU342753	This study
<i>G. multiporum</i>	RSP05-41	<i>Juniperus monosperma</i>	III	KJ720179 ^b			Novick (2008)
<i>G. nelsonii</i>	CUP-55918	<i>Crataegus brunnatiana</i>	0,1	MN642600	MN642595	MN642619	This study
	DAOM226326	<i>Juniperus horizontalis</i>	III	KJ720166 ^b			Novick (2008)
	RSP01-237	<i>Juniperus horizontalis</i>	III	KJ720163 ^b			Novick (2008)
	RSP 99-93	<i>Juniperus horizontalis</i>	III	KJ720180 ^b			Novick (2008)
	NYBG193254	<i>Juniperus horizontalis</i>	III	MN605011	KU288663	KU342740	This study
	NYBG193243	<i>Juniperus horizontalis</i>	III	MN605012	KU288653	KU342739	This study
	NYBG199427	<i>Juniperus horizontalis</i>	III	MN605013	-	-	This study
	NYBG638372	<i>Juniperus scopulorum</i>	III	MN642599	MN642594	MN642618	This study
	BPI 880709	<i>Amelanchier alnifolia</i>	0,1	-		HM591299	Schilder et al. (2011)
	ZP-R83	<i>Malus</i> sp.	0,1	MK488097	MK518808	MK518447	This study
	<i>G. nidus-avis</i>	CUP-227	<i>Amelanchier</i> sp.	0,1	MN605014	MN605719	MN605797
NYBG461234		<i>Juniperus juvenescens</i>	III	MN605015	KU288701	KU342758	This study
NYBG237071		<i>Juniperus virginiana</i>	III	MN605016	KU288688	KU342762	This study
HMAS14429		<i>Juniperus virginiana</i>	III	MN605017	MN605720	MN605798	This study
NYBG237094		<i>Juniperus virginiana</i>	III	MN605018	KU288686	KU342755	This study
NYBG237080		<i>Juniperus virginiana</i>	III	MN605019	KU288700	KU342757	This study
NYBG14419		<i>Juniperus virginiana</i>	III	MN605020	KU288681	KU342756	This study
RSP 05-29		<i>Juniperus virginiana</i>	III	KJ720181 ^b			Novick (2008)
NYBG461235		<i>Malus communis</i>	0,1	MN605021	-	-	This study
TNM F0030470		<i>Photinia nitakayamensis</i>	0,1	KY964759 ^b			Shen et al. (2018)
TNM F0027944		<i>Photinia nitakayamensis</i>	0,1	KP308395 ^b			Shen et al. (2018)
TNM F0030464	<i>Photinia nitakayamensis</i>	0,1	KY964758 ^b			Shen et al. (2018)	
TNM F0030474	<i>Photinia nitakayamensis</i>	0,1	KY964760 ^b			Shen et al. (2018)	
<i>G. nipponicum</i>	HMAS 31297	<i>Sorbus alnifolia</i>	0,1	KJ720182 ^b			Novick (2008)
<i>G. nootkatense</i>	PUR 63656	<i>Juniperus virginiana</i>	III	KJ720159 ^b			Novick (2008)

Table S2 (cont.)

Species	Specimen No. ^a	Host	Spore stage	GenBank Accession No. ^b			References
				SSU	ITS	LSU	
<i>G. przewalskii</i>	BJFC-R01859	<i>Juniperus koehneana</i>	0,1	—	NR_154073	KR814560	Cao et al. (2017)
	BJFC-R02084	<i>Juniperus koehneana</i>	0,1	—	KX528447	KX814560	Cao et al. (2017)
	BJFC-R02083	<i>Juniperus przewalskii</i>	III	—	KX528446	KX528444	Cao et al. (2017)
	BJFC-R01860	<i>Juniperus przewalskii</i>	III	—	KR814564	KR814561	Cao et al. (2017)
	DB 1548	<i>Juniperus chinensis</i>	III	—	—	AY512845	Begerow et al. (unpubl.)
	RN43	<i>Juniperus chinensis</i>	III	KJ720183 ^b	—	—	Novick (2008)
	20140331-6	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	III	—	KM403109	—	Fernández & Alvarado (unpubl.)
	20140331-7	<i>Juniperus phoenicea</i> subsp. <i>turbinata</i>	III	—	KP261044	—	Fernández & Alvarado (unpubl.)
	CUP-0477	<i>Juniperus sabina</i>	III	MN605022	MN605721	MN605799	This study
	20150325-2-M2	<i>Juniperus oxycedrus</i>	III	—	KT160252	—	Fernández & Alvarado (2016)
20140330-3 M2	<i>Juniperus oxycedrus</i>	III	—	—	—	Fernández & Alvarado (2016)	
BG1	<i>Juniperus</i> sp.	III	KM403110 ^b	—	—	Filipp & Spornberger (unpubl.)	
BG2	<i>Juniperus</i> sp.	III	KF925316 ^b	—	—	Filipp & Spornberger (unpubl.)	
BG3	<i>Juniperus</i> sp.	III	KF925317 ^b	—	—	Filipp & Spornberger (unpubl.)	
BG4	<i>Juniperus</i> sp.	III	KF925318 ^b	—	—	Filipp & Spornberger (unpubl.)	
BG5	<i>Juniperus</i> sp.	III	KF925319 ^b	—	—	Filipp & Spornberger (unpubl.)	
BG6	<i>Juniperus</i> sp.	III	KF925320 ^b	—	—	Filipp & Spornberger (unpubl.)	
	<i>Juniperus</i> sp.	III	KF925321 ^b	—	—	Filipp & Spornberger (unpubl.)	
TNM F0030476	<i>Pyrus amygdaliformis</i>	0,1	KY964763 ^b	—	—	Shen et al. (2018)	
GYMSAB 0004	<i>Pyrus calleryana</i>	0,1	—	—	JN969965	Kenaley et al. (2012)	
BPI 893287	<i>Pyrus calleryana</i>	0,1	KU593568 ^b	—	—	Hansen (unpubl.)	
GYMSAB 0001	<i>Pyrus communis</i>	0,1	—	—	JN969962	Kenaley et al. (2012)	
20140923 H2	<i>Pyrus communis</i>	0,1	—	KP261039	—	Fernández & Alvarado (2016)	
GYMSAB 0005	<i>Pyrus communis</i>	0,1	—	—	JN969966	Kenaley et al. (2012)	
20141009	<i>Pyrus communis</i>	0,1	—	KP261040	—	Fernández & Alvarado (2016)	
LD 1022	<i>Pyrus communis</i>	0,1	HM114221 ^b	—	—	Dervis (unpubl.)	
TNM F0030477	<i>Pyrus communis</i>	0,1	KY964764 ^b	—	—	Shen et al. (2018)	
GYMSAB 0003	<i>Pyrus communis</i>	0,1	—	—	JN969964	Kenaley et al. (2012)	
WM 1347	<i>Pyrus communis</i>	0,1	—	—	AF426209	Maier et al. (2003)	
GYMSAB 0002	<i>Pyrus communis</i>	0,1	—	—	JN969963	Kenaley et al. (2012)	
<i>G. shennongjiaense</i>	ZP-R420	<i>Malus asiatica</i>	0,1	MN605023	MK518924	MK518604	This study
	ZP-R511	<i>Malus asiatica</i>	0,1	MN605024	MN605722	MN605800	This study
	HMAS55353	<i>Malus</i> sp.	0,1	MN605025	MN605723	MN605801	This study
	ZP-R627	<i>Malus</i> sp.	0,1	—	MN605724	MN605802	This study
RSP99-96	<i>Juniperus virginiana</i>	III	KJ720160 ^b	—	—	Novick (2008)	
<i>G. speciosum</i>	HMAS26416	<i>Malus spectabilis</i>	0,1	MN605030	MN605727	MN605805	This study
	HMAS248124	<i>Malus</i> sp.	0,1	MN605026	MN605725	MN605803	This study
<i>G. tiankengense</i>	ZP-R1375	<i>Malus</i> sp.	0,1	MN605027	MN605726	MN605804	This study
	20170805	<i>Sorbus torminalis</i>	0,1	—	MG572220	—	Fernández & Alvarado (unpubl.)
<i>G. torminalis-juniperini</i>	NYBG3009468	<i>Juniperus virginiana</i>	III	MN605031	MN605728	MN605806	This study
	BPI 910169	<i>Juniperus virginiana</i>	III	KY798387 ^b	—	—	Demers (unpubl.)
	RN 91	<i>Juniperus virginiana</i>	III	KJ720184 ^b	—	—	Novick (2008)
<i>G. tremelloides</i>	BPI 910170	<i>Pyrus calleryana</i>	0,1	KY798388 ^b	—	—	Demers (unpubl.)
	NYBG23203	<i>Amelanchier</i> sp.	0,1	MN605028	KU288639	KU342768	This study
<i>G. tsingchenensis</i>	CPO 18.03	<i>Juniperus deppiana</i>	III	KM382069	—	—	Nieto-Lopez (unpubl.)
	CUP-43859	<i>Malus communis</i>	0,1	MN605029	KU288680	KU342769	This study
	HMAS133735	<i>Cupressus funebris</i>	III	MN605032	—	—	This study

Table S2 (cont.)

Species	Specimen No. ^a	Host	Spore stage	GenBank Accession No. ^c			References
				SSU	ITS	LSU	
<i>G. vauquelinae</i>	RSP05-87	<i>Vauquelinia angustifolia</i>	0,1	KJ720186 ^b			Novick (2008)
<i>G. yamadae</i>	CUP-776	<i>Aroma atropurpurea</i>	0,1	MN605033	MN605729	MN605807	This study
	BPI 893269	<i>Crataegus</i> sp.	0,1	KY798356 ^b			Demers (unpubl.)
	NYBG3009549	<i>Juniperus chinensis</i>	III	MN605034	MN605730	MN605808	This study
	HKFRI 2000	<i>Juniperus chinensis</i>	III			FJ559375	Yun et al. (2009)
	HKFRI 2001	<i>Juniperus chinensis</i>	III	KJ720187 ^b			Novick (2008)
	PQ05009	<i>Juniperus chinensis</i>	III	GU058012 ^b			Dixon et al. (2010)
	BJFC-R01822	<i>Juniperus chinensis</i>	III		KR814566	KT719163	Cao et al. (2016)
	BJFC-R01823	<i>Juniperus chinensis</i>	III		KR814567	KT719164	Cao et al. (2016)
	HMA547229	<i>Juniperus chinensis</i>	III	MN605035	MN605731	MN605809	This study
	HMA582779	<i>Juniperus chinensis</i>	III	MN605036	KJ288646	KU342730	This study
	HKFRI 2002	<i>Juniperus chinensis</i> cv. <i>kaizuka</i>	III			FJ848763	Yun et al. (2009)
	HMAS143619	<i>Juniperus chinensis</i> cv. <i>kaizuka</i>	III	MN605037	KJ288649	KU342742	This study
	HMA580528	<i>Malus baccata</i>	0,1	MN605038	MN605732	MN605810	This study
	HMA555351	<i>Malus baccata</i>	0,1	MN605039			This study
	LIG_1	<i>Malus micromalus</i>	0,1	MN605040	MN605733	MN605811	This study
	LIG_2	<i>Malus micromalus</i>	0,1	MN605041	KU288660	KU342728	This study
	LIG_3	<i>Malus micromalus</i>	0,1	MN605042	KU288638	KU342729	This study
	LIG_4	<i>Malus micromalus</i>	0,1	MN605043	KU288666	KU342725	This study
	HMA5243188	<i>Malus micromalus</i>	0,1	MN605044	KU288659	KU342726	This study
	HMA555352	<i>Malus micromalus</i>	0,1		KU288695	KU342727	This study
	CUP-20612	<i>Malus micromalus</i>	0,1	MN605045	MN605734	MN605812	This study
	HMA5199333	<i>Malus micromalus</i>	0,1	MN605046	KU288674	KU342724	This study
	ZP-R16	<i>Malus micromalus</i>	0,1				This study
	NYBG2584	<i>Malus miura</i>	0,1	MN605048	MN605735	MN605813	This study
	HMA536992	<i>Malus prunifolia</i>	0,1	MN605049	KU288662	KU342732	This study
	NYBG53757	<i>Malus toring</i>	0,1	MN605050	MN605736	MN605814	This study
	ZP-R633	<i>Malus</i> sp.	0,1	MN605052	MN605737	MN605815	This study
	ZP-R634	<i>Malus</i> sp.	0,1	MN605053	MN605738	MN605816	This study
	ZP-R635	<i>Malus</i> sp.	0,1	MK488462	MK519020	MK518722	This study
	ZP-R637	<i>Malus</i> sp.	0,1	MK488413	MK518995	MK518699	This study
	NYBG53751	<i>Malus spectabilis</i>	0,1	MN605051			This study
	HMA530992	<i>Malus prunifolia</i>	0,1	MN605054	MN605739	MN605817	This study
<i>Gymnosporangium</i> sp. 1	HMA579065	<i>Juniperus chinensis</i>	III		KU288684	KU342721	This study
	HMA5135611	<i>Juniperus chinensis</i>	III		KU288699	KU342736	This study
	DAQM 234634	<i>Juniperus scopulorum</i>	III	HQ317506			Liu et al. (2015)
	R046	<i>Pyrus</i> sp.	0,1	KY800408			Demers (unpubl.)
<i>Gymnosporangium</i> sp. 2	LD 1021	<i>Crataegus mongyna</i>	0,1	HM114219			Demers (unpubl.)
	20140618	<i>Crataegus mongyna</i>	0,1			KP261045	Fernández & Alvarado (2016)
	HMA552880	<i>Cotoneaster melanocarpus</i>	0,1	MN605055	MN605740	MN605818	This study
	DAQM220748	<i>Cotoneaster melanocarpus</i>	0,1	KJ720165 ^b			Novick (2008)
	LD1015	<i>Juniperus</i> sp.	III	GU058011 ^b			Dixon et al. (2010)
	CUP-2613	<i>Malus</i> sp.	0,1	MN605056	MK518910	MK518582	This study
<i>Gymnosporangium</i> sp. 3	ZP-R1389	<i>Chamaecyparis</i> sp.	III	MN605057	MN605741	MN605819	This study
<i>Endoraeicum tropicum</i>	BRIP66557	<i>Acacia tropica</i>	III	KJ862417	KJ862392	KJ862337	McTaggart et al. (2015)

^a CUP: Plant Pathology Herbarium, Cornell University, Ithaca, New York, USA; HMAS: The Mycological Herbarium of Institute of Microbiology, CAS, China; NYBG: New York Botanical Garden, New York, USA; NYS: New York State Museum, New York, USA; ZP: Personal collection by Peng Zhao.

^b represents the specimens with SSU, ITS and LSU sequence together.

^c Sequence data generated from this study were listed in bold format.

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