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Article

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Cronartium rust (*Pucciniales*, *Cronartiaceae*): species delineation, diversity and host alternation

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Abstract

Cronartium species (*Basidiomycota*, *Pucciniales*, *Melampsorineae*) infect two or five-needle pines, resulting in considerable economic losses and ecological damage. Many species are considered of quarantine importance, however, precise identification is challenging due to the poorly resolved generic boundaries of *Cronartium* and other members in *Melampsorineae*, as well as species limits within the genus *Cronartium*. In this study, species delimitation was carried out based on morphological examination and multi-locus phylogenetic assessment using sequences of rDNA SSU-ITS-LSU regions and CO3 gene. Twenty-six species including seven new species (*C. castaneae*, *C. mongolicum*, *C. murrayanae*, *C. myricae*, *C. peridiatum*, *C. qinlingense*, *C. ribis-taedae*), and one new combination (*C. floridanum*) are recognized. *Cronartium arizonicum*, *C. comandrae*, *C. comptoniae*, *C. occidentale*, and *C. pyriforme* are epitypified to stabilize the use of names for taxonomy and quarantine significance. In addition, 18 species were revealed for their previously unknown life cycles.

Keywords – pine blister rust – *Pucciniales* – quarantine pests – species boundary – taxonomy

Introduction

Cronartium is a genus of biotrophic, obligate plant-parasitic rusts in the *Cronartiaceae* family (*Pucciniales*, *Basidiomycota*) that causes pine blister rust epidemics, resulting in severe economic losses and ecological damage in temperate regions in the Northern Hemisphere (Millar & Kinloch 1991, McDonald & Hoff 2001, Zhang et al. 2010). Many species, such as *C. coleosporioides*, *C. comandrae*, *C. comptoniae*, *C. fusiforme*, *C. harknessii*, *C. himalayense*, *C. quercuum*, and *C. ribicola*, have been listed as quarantine pests in numerous countries (EPPO 2019, 2021). Species in the whole *Cronartiaceae* family are listed as quarantine targets of the United States (https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/rppl/rppl-table). For phytosanitary and disease control, accurate identification and efficient monitoring of these pests are critical. *Cronartium* species, on the other hand, are notoriously difficult to identify. They have different and complicated life cycles with either two, three or five spore stages and alternate between two taxonomically unrelated host plants, usually *Pinus* species and another one of eight other plant families, *Asclepiadaceae*, *Fagaceae*, *Gentianaceae*, *Myricaceae*, *Paeoniaceae*, *Santalaceae*, *Saxifagaceae* and *Scrophulariaceae* (Peterson 1967, Cummins & Hiratsuka 1983,

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2003). In addition, taxonomies at the family, genus, and species levels have long been in a state of confusion, and most *Cronartium* species lack definite distinguishable morphological criteria and DNA information (Hiratsuka 1995, Qi et al. 2019, Wijesinghe et al. 2019).

Since the establishment of *Cronartium* based on the type species *C. asclepiadeum* (Fries 1815), it has undergone multiple taxonomic reassignments at different ranks. At the family level, *Cronartium* was initially classified as a member of the *Pucciniaceae* until *Cronartiaceae* was established (Dietel 1897, 1928). It was then classified as a member of the *Cronartiaceae*, *Coleosporiaceae*, *Melampsoraceae* or *Pucciniastraceae* (Dietel 1928, Cummins & Hiratsuka 1983, 2003, Aime & McTaggart 2021). Although molecular phylogenetic studies have confirmed the placement of *Cronartium* in the suborder *Melampsorineae* (Aime 2006, Aime & McTaggart 2021), its relationship with other genera in *Melampsorineae*, particularly *Pucciniastrum*, *Quasipucciniastrum*, and *Thekopsora*, has not been well resolved (Maier et al. 2003, Wingfield et al. 2004, Aime et al. 2018a, Qi et al. 2019, Zhao et al. 2020, 2021a). Aime & McTaggart (2021) presented a high-rank classification of *Pucciniales*, and *Cronartium* was classified, along with several other genera, including *Chrysomyxa*, *Coleosporium*, *Diaphanopellis*, *Quasipucciniastrum*, *Rossmanomyces*, and *Thekopsora* in the *Coleosporiaceae* based on their aecial similarity. However, they showed significant morphological differences in spermogonia and telia, which have long been used as major criteria for family classification (Cummins & Hiratsuka 1983, 1984, 2003). As a result, the taxonomic placement of *Cronartium* remains a point of contention, and it is necessary to reassign *Cronartium* and related genera to the correct family.

At the generic level, 68 *Cronartium* epithets (not including varieties and *formae speciales*) have been documented in Index Fungorum (www.indexfungorum.org). By emphasizing morphological differences of spermogonia and telia, and the type of life cycle, Peterson (1973) assigned 19 species to the genera *Cionothrix*, *Crossopsora*, *Didymopsora* or *Dietelia*. Such taxonomic treatment was justified because the phylogenetic separation of these four genera from *Cronartium* and other members in *Melampsorineae* had already been verified (Aime et al. 2018a, Qi et al. 2019, Zhao et al. 2020, Aime & McTaggart 2021). Based on morphologies in aecia and telia or the type of life cycle, the remaining *Cronartium* species have been classified into three genera, *Cronartium*, *Endocronartium* and *Peridermium* (Hiratsuka 1969, 1971, 1995). Such taxonomic arrangement was not universally accepted because several *Endocronartium* species had comparable morphologies and phylogenetic affinities with *Cronartium* species (Vogler & Bruns 1998, Kim et al. 2010). Thus, it was suggested that species in *Endocronartium* and some *Peridermium* species found on pines should be assigned to *Cronartium* (Aime et al. 2018b). *Cronartium* now contains 24 legitimate species (Aime et al. 2018b), but many identities have yet to be confirmed.

Some previous researchers used morphological features or host information to define the species, while others grouped multiple taxa under a single name that reflected a species complex by emphasizing morphological similarities (Hiratsuka 1995). So far, *C. coleosporioides*, *C. comandrae*, *C. flaccidum*, *C. quercuum* and *C. ribicola*, were listed as five species complexes, but the taxa within each complex differed among taxonomists (Hiratsuka 1995). Consequently, there is confusion when it comes to inspection and designation of species, especially for those of quarantine significance (Peterson & Jewell 1968, Burdsall & Snow 1977, Imazu et al. 1989, Millar & Kinloch 1991, Kaitera 2011). Several studies have shown that morphological features of uredinia and telia are insufficient to recognize cryptic taxa in these complexes, especially as inoculation experiments and molecular studies have frequently revealed the presence of such species (Kaneko 2000, Richardson et al. 2009). Rigorous taxonomic investigations are urgently needed to define species boundaries within *Cronartium*, especially for those species complexes listed as significant quarantine targets in Europe and Asian countries.

In this study, 1032 specimens from *Cronartium* and allied genera were analyzed in order to revise the taxonomy of *Cronartium* and to elucidate alternate hosts of several key species, especially those quarantine targets in China, EPPO and other north hemisphere countries.

Materials & Methods

Specimens examined in this study

A total of 1032 herbarium specimens were borrowed from fungaria to cover the largest number of hosts based on taxonomic literature (Peterson 1967, 1973, Hirastuka 1995, Farr & Rossman 2021). These included Ada Hayden Herbarium, Iowa State University, Iowa, USA (ISC); Herbarium, Kunming Institute of Botany, CAS, China (HKAS); Mycological Herbarium of Institute of Microbiology, CAS, China (HMAS); New York Botanical Garden, New York, USA (NYBG); New York State Museum, New York, USA (NYS); Plant Pathology Herbarium, Cornell University, Ithaca, New York, USA (CUP); Plant Pathology Herbarium, University of Tsukuba, Tsukuba, Japan (TSH); University of British Columbia Herbarium, British Columbia, Canada (UBC); University of Florida Herbarium, Florida Museum of Natural History, Florida, USA (FLAS) and University of Michigan Herbarium, University of Michigan, Michigan, USA (MICH). The names on the attached labels and host information were used to select specimens with either aecial or telial stage; This resulted in 235 specimens from *Pinus* species and 797 from eight other plant families, i.e., *Asclepiadaceae*, *Fagaceae*, *Gentianaceae*, *Myricaceae*, *Paeoniaceae*, *Santalaceae*, *Saxifagaceae* and *Scrophulariaceae*.

Molecular phylogeny and species delimitation

Rust sori were excised from each specimen, and DNA was extracted using the Gentra Puregene Tissue Kit (Qiagen, Valencia, CA) according to the manufacturer's instructions. To investigate the phylogenetic position of each taxon, three nuclear ribosomal RNA gene regions, i.e., 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 nested PCR method was employed to improve the amplification. The primer sequences and annealing temperatures of these target regions were described in detail in Zhao et al. (2015, 2016, 2017). Besides, the cytochrome c oxidase subunit 3 (CO3) in the mitochondrial genome was amplified with the primers CO3_F1/CO3_R1 (Beenken et al. 2012).

The SSU, ITS, LSU, and CO3 sequences were generated from 278 specimens. Raw sequence data were aligned by Bioedit v. 7.0.9 (Hall 1999). The newly generated sequences in this study were deposited in GenBank, and herbarium numbers, host species, geographical origins, and GenBank accession numbers of these specimens used for phylogenetic studies are listed in Table 1. The dataset comprised aligned sequences of SSU, ITS, LSU, and CO3 from *Cronartium* specimens. Two *Endoraecium* species were selected as outgroups. For phylogenetic analyses, 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. 2019). Ambiguous alignment positions were adjusted manually and ambiguous sites were excluded for the final analyses. 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 (BYPP) 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 features of each specimen were observed using a dissecting microscope (SMZ745, Nikko, Japan), light microscope (Axio Imager A2, ZEISS, Germany), and scanning electron microscope (Hitachi SU8010200, Tokyo, Japan) based on the outline of Zhao et al. (2015, 2017). Morphological characteristics were compared with the type specimens, original descriptions, and other published descriptions of the species involved (e.g., Sydow & Sydow 1915, Arthur 1934, Kuprevich & Tranzschel 1957, Wilson & Henderson 1966, Peterson 1967, 1973, 1974, 1982, Hiratsuka et al. 1992). Different spore stages of rust fungi were designated by following.

Table 1 Species and specimens of *Cronartium*, and GenBank accession numbers of sequences used for phylogenetic studies at species level. Sequences in bold were generated in this study.

Species	**Specimen No.**[a]	**Spore stage**	**Host**	**Country**	**GenBank Accession No.**[a]			
					SSU	**ITS**	**LSU**	**CO3**
C. appalachianum	Ca-1	0, I	*Pinus virginiana*	USA	–	L76484	–	–
C. arizonicum	MICH253346	II, III	*Castilleja linariaefolia*	USA	**OM745897**	MK208284	MK193824	**OM721322**
	MICH301231	0, I	*P. ponderosa*	USA	**OM745898**	**OM746340**	**OM746508**	**OM721323**
	HMAS54853	0, I	*P. ponderosa*	USA	**OM745899**	**OM746341**	**OM746509**	**OM721324**
	MICH300079	0, I	*P. ponderosa*	USA	**OM745900**	**OM746342**	**OM746510**	**OM721325**
	MICH301493	0, I	*P. ponderosa*	USA	**OM745901**	**OM746343**	**OM746511**	**OM721326**
	MICH300081	0, I	*P. ponderosa*	USA	**OM745902**	MK208299	MK193831	**OM721327**
	MICH300080	0, I	*P. ponderosa*	USA	**OM745903**		**OM746512**	**OM721328**
	FSprP- 1	0, I	*P. ponderosa*	USA	–	L76504	–	–
C. armandii	HMAS79166	II, III	*Ribes maximowiczii*	China	**OM745904**	MZ520620	MZ520623	**OM721329**
	HMAS64281	II, III	*R. orientale*	China	**OM745905**	**OM746344**	MZ520623	**OM721330**
	HMAS64280	II, III	*R. orientale*	China	**OM745906**	**OM746345**	**OM746513**	**OM721331**
	HMAS64278	II, III	*R. griffithii*	China	**OM745907**	**OM746346**	**OM746514**	**OM721332**
	HMAS64277	II, III	*R. griffithii*	China	**OM745908**	**OM746347**	**OM746515**	**OM721333**
	HMAS64390	II, III	*Ribes* sp.	China	**OM745909**	**OM746348**	**OM746516**	**OM721334**
	ZP-R901	II, III	*Ribes* sp.	China	**OM745910**	**OM746349**	**OM746517**	**OM721335**
	HMAS45350	0, I	*P. armandii*	China	**OM745911**	MZ520620	MZ520623	OM721336
	HMAS56424	0, I	*P. armandii*	China	**OM745912**	**OM746351**	**OM746519**	**OM721337**
	HKAS9613	0, I	*P. corensis*	China	**OM745913**	**OM746352**	**OM746520**	**OM721338**
	Hsh2	0, I	*P. armandii*	China	–	EU826971	–	–
C. bethelii	MICH253453	II, III	*Q. emoryi*	USA	**OM745914**	**OM746353**	**OM746521**	**OM721339**
	HMAS82418	II, III	*Q. mongolica*	China	**OM745915**	**OM746354**	**OM746522**	**OM721340**
	CrKor-1	0, I	*P. strobus*	USA	–	L76497	–	–
	FLAS-F-16608	0, I	*P. palustris*	USA	**OM745916**	**OM746355**	**OM746523**	**OM721341**
C. castaneae	HMAS18841	II, III	*Castanea* sp.	China	**OM745917**	**OM746356**	**OM746524**	**OM721342**
	HMAS8970	0, I	*P. ponderosa*	USA	**OM745918**	**OM746357**	**OM746525**	**OM721343**
C. coleosporioides	CsSr-1	0, I	*P. contorta*	USA	–	L76500	–	–
	SHmC-9	0, I	*P. contorta*	USA	–	L76511	–	–
	SPC-21	0, I	*P. contorta* var. *latifolia*	USA	–	L76513	–	–
C. comandrae	HMAS24619	II, III	*Comandra richardsiana*	Canada	**OM745919**	**OM746358**	**OM746526**	**OM721344**
	ISC250404	II, III	*Com. umbellata*	USA	**OM745920**	**OM746359**	**OM746527**	**OM721345**
	ISC391495	II, III	*Com. umbellata*	USA	**OM745921**	**OM746360**	**OM746528**	**OM721346**

Table 1 Continued.

Species	**Specimen No.**[a]	**Spore stage**	**Host**	**Country**	**GenBank Accession No.**[a]			
					SSU	**ITS**	**LSU**	**CO3**
	ISC392260	II, III	*Com. pallida*	USA	**OM745922**	**OM746361**	**OM746529**	**OM721347**
	ISC392261	II, III	*Com. pallida*	USA	**OM745923**	**OM746362**	**OM746530**	**OM721348**
	ISC395244	II, III	*Com. umbellata*	USA	**OM745924**	**OM746363**	**OM746531**	**OM721349**
	ISC395247	II, III	*Com. umbellata*	USA	**OM745925**	**OM746364**	**OM746532**	**OM721350**
	HC-H5-FP	II, III	*Com. pallida*	Canada	–	JN943210	–	–
	MV-J9-FP	II, III	*Com. pallida*	Canada	–	JN943211	–	–
	MICH253330	II, III	*Com. pallida*	USA	**OM745926**	**OM746365**	**OM746533**	**OM721351**
	MICH253364	II, III	*Com. umbellata*	USA	**OM745927**	MK208293	MK193825	**OM721352**
	MICH253430	II, III	*Com. pallida*	USA	**OM745928**	**OM746366**	**OM746534**	**OM721353**
	MICH253516	II, III	*Com. pallida*	USA	**OM745929**	**OM746367**	**OM746535**	**OM721354**
	MICH253517	II, III	*Com. pallida*	USA	**OM745930**	**OM746368**	**OM746536**	**OM721355**
	NYBG267638	II, III	*Com. richardsiana*	USA	**OM745931**	MK208294	MK193826	**OM721356**
	NYBG3106200	II, III	*Com. pallida*	USA	**OM745932**	MK208295	MK193827	**OM721357**
	NYBG3106202	II, III	*Com. pallida*	USA	**OM745933**	**OM746369**	**OM746537**	**OM721358**
	UBC-F5867	II, III	*Com. pallida*	USA	**OM745934**	**OM746370**	**OM746538**	**OM721359**
	UBC-F5869	II, III	*Com. pallida*	Canada	**OM745935**	**OM746371**	**OM746539**	**OM721360**
	MICH253419	II, III	*Comandra* sp.	USA	**OM745936**	**OM746372**	**OM746540**	**OM721361**
	NYBG3106199	II, III	*Comandra* sp.	USA	**OM745937**	**OM746373**	**OM746541**	**OM721362**
	CcND-1	0, I	*P. contorta*	USA	–	U75985	–	–
	BCpC-15	0, I	*P. contorta*	USA	–	L76477	–	–
	BLvC-8	0, I	*P. contorta*	USA	–	L76478	–	–
	CGcC-21	0, I	*P. contorta*	USA	–	L76480	–	–
	CPeEl-1	0, I	*P. eldarica*	USA	–	L76481	–	–
	CWC-9	0, I	*P. contorta*	USA	–	L76483	–	–
	UBC-F5868	0, I	*P. banksiana*	Canada	**OM745938**	**OM746374**	**OM746542**	**OM721363**
	Cc-1	0, I	*Pinus* sp.	USA	–	L76485	–	–
	NYBG36363	0, I	*Pinus* sp.	USA	**OM745938**	**OM746374**	**OM746542**	**OM721363**
	NYBG36381	0, I	*Pinus* sp.	USA	**OM745939**	**OM746375**	**OM746543**	**OM721364**
	42CR-PNB-RN6	0, I	Host unknown	Canada	–	JN943242	–	–
C. comptoniae	UBC-F5871	II, III	*Comptonia peregrina*	USA	**OM745941**	**OM746377**	**OM746545**	**OM721366**
	UBC-F5870	II, III	*Co. asplenitolia*	USA	**OM745942**	**OM746378**	**OM746546**	**OM721367**
	ISC351966	II, III	*Co. peregrina*	USA	**OM745943**	**OM746379**	**OM746547**	**OM721368**
	ISC391579	II, III	*Co. peregrina*	USA	**OM745944**	**OM746380**	**OM746548**	**OM721369**

Table 1 Continued.

Species	Specimen No.[a]	Spore stage	Host	Country	GenBank Accession No.[a]			
					SSU	ITS	LSU	CO3
	MICH253508	II, III	*Co. peregrina*	Canada	**OM745945**	**OM746381**	**OM746549**	**OM721370**
	CcomMn-1	II, III	*Comptonia* sp.	USA	–	L76487	–	–
	1148CRT-PNB-LJ	II, III	*Comptonia* sp.	Canada	–	JN943254	–	–
	BLD-B6-FP	II, III	*Comptonia* sp.	Canada	–	JN943209	–	–
	INC-1-FP	II, III	*Comptonia* sp.	Canada	–	JN943208	–	–
	MICH253506	0, I	*P. banksiana*	Canada	**OM745946**	**OM746382**	**OM746550**	**OM721371**
C. flaccidum	FLAS-F-55559	II, III	*Paeonia officinalis*	Finland	**OM745947**	**OM746383**	**OM746551**	**OM721372**
	HKAS46625	II, III	*Pae. lactiflora*	China	**OM745948**	**OM746384**	**OM746552**	**OM721373**
	HMAS133885	II, III	*Pae. lactiflora*	China	**OM745949**	**OM746385**	**OM746553**	**OM721374**
	HMAS199449	II, III	*Pae. delaveyi*	China	**OM745950**	**OM746386**	**OM746554**	**OM721375**
	HMAS199451	II, III	*Pae. delaveyi*	China	**OM745951**	**OM746387**	**OM746555**	**OM721376**
	HMAS199453	II, III	*Pae. delaveyi*	China	**OM745952**	**OM746388**	**OM746556**	**OM721377**
	HMAS37551	II, III	*Pae. lactiflora*	China	**OM745953**	**OM746389**	**OM746557**	**OM721378**
	HMAS67474	II, III	*Pae. lactiflora*	China	**OM745954**	**OM746390**	**OM746558**	**OM721379**
	HMAS74263	II, III	*Pae. lactiflora*	Russia	**OM745955**	**OM746391**	**OM746559**	**OM721380**
	HMAS82718	II, III	*Pae. lactiflora*	Russia	**OM745956**	**OM746392**	**OM746560**	**OM721381**
	HMAS82720	II, III	*Pae. lactiflora*	Russia	**OM745957**	**OM746393**	**OM746561**	**OM721382**
	HMAS89228	II, III	*Pae. lactiflora*	Russia	**OM745958**	**OM746394**	**OM746562**	**OM721383**
	HMAS89229	II, III	*Pae. lactiflora*	Russia	**OM745959**	MK208286	MK193819	**OM721384**
	HMAS89230	II, III	*Pae. lactiflora*	Russia	**OM745960**	–	–	**OM721385**
	HMAS89231	II, III	*Pae. lactiflora*	China	**OM745961**	MK208289	MK193822	**OM721386**
	HMAS89232	II, III	*Pae. lactiflora*	China	**OM745962**	**OM746396**	**OM746564**	**OM721387**
	MICH253449	II, III	*Pae. officinalis*	Finland	**OM745963**	**OM746397**	**OM746565**	**OM721388**
	HMAS243693	II, III	*Paeonia* sp.	UK	**OM745964**	**OM746398**	**OM746566**	**OM721389**
	FLAS-F-39572	II, III	*Paeonia* sp.	USA	**OM745965**	**OM746399**	**OM746567**	**OM721390**
	HMAS243702	II, III	*Paeonia* sp.	UK	**OM745966**	**OM746400**	**OM746568**	**OM721391**
	ISC351967	II, III	*Paeonia* sp.	USA	**OM745967**	**OM746401**	**OM746569**	**OM721392**
	MICH253441	II, III	*Paeonia* sp.	Romania	**OM745968**	**OM746402**	**OM746570**	**OM721393**
	HMAS76249	II, III	*Vincetoxicum hirundinaria*	Germany	**OM745969**	**OM746403**	**OM746571**	**OM721394**
	HMAS77682	0, I	*P. massoniana*	China	**OM745970**	**OM746404**	**OM746572**	**OM721395**
	HMAS44164	0, I	*P. taiwanensis*	China	**OM745971**	MK208288	MK193816	**OM721396**

Table 1 Continued.

Species	Specimen No.[a]	Spore stage	Host	Country	GenBank Accession No.[a]			
					SSU	ITS	LSU	CO3
	HMAS82784	0, I	*P. tabulaeformis*	China	**OM745972**	MK208287	MK193818	**OM721397**
	CUP-458	0, I	*P. silvestris*	USA	**OM745973**	**OM746405**	**OM746573**	**OM721398**
	MICH300082	0, I	*P. ponderosa*	USA	**OM745974**	–	–	–
	UBC-F1355	0, I	*P. contorta* var. *latifolia*	USA	**OM745975**	**OM746406**	**OM746574**	**OM721399**
	UBC-F1363	0, I	*P. ponderosa*	USA	**OM745947**	**OM746407**	**OM746575**	**OM721400**
C. floridanum	MICH299992	0, I	*P. palustris*	USA	**OM745976**	**OM746408**	**OM746576**	**OM721401**
	MICH300092	0, I	*P. palustris*	USA	**OM745977**	**OM746409**	**OM746577**	**OM721402**
C. fusiforme	HMAS2141	II, III	*Cyanchum nigrum*	Sweden	**OM745978**	**OM746410**	**OM746578**	**OM721403**
	HMAS1148	II, III	*Q. serrata*	Japan	**OM745979**	**OM746411**	**OM746579**	**OM721404**
	HMAS31283	II, III	*Q. variabilis*	China	**OM745980**	**OM746412**	**OM746580**	**OM721405**
	HMAS41540	II, III	*Q. fabri*	China	**OM745981**	**OM746413**	**OM746581**	**OM721406**
	HMAS55095	II, III	*Q. variabilis*	China	**OM745982**	**OM746414**	**OM746582**	**OM721407**
	HMAS56356	II, III	*Q. variabilis*	China	**OM745983**	**OM746415**	**OM746583**	**OM721408**
	HMAS71281	II, III	*Q. variabilis*	China	**OM745984**	**OM746416**	**OM746584**	**OM721409**
	HMAS74355	II, III	*Q. variabilis*	China	**OM745985**	**OM746417**	**OM746585**	**OM721410**
	HMAS9043	II, III	*Q. emoryii*	USA	**OM745986**	**OM746418**	**OM746586**	**OM721411**
	HMAS35526	II, III	*Quercus* sp.	China	**OM745987**	**OM746419**	**OM746587**	**OM721412**
	HMAS52087	0, I	*P. silvestris*	China	**OM745988**	**OM746420**	**OM746588**	**OM721413**
C. keteleeriae	HMAS11129	0, I	*Keteleeria davidiana*	China	**OM745989**	**OM746421**	**OM746588**	**OM721414**
	HMAS638	0, I	*K. davidiana*	China	**OM745990**	**OM746422**	–	**OM721415**
C. mongolicum	HMAS242639	II, III	*Q. mongolica*	China	**OM745991**	**OM746423**	–	–
	ZP-R7	II, III	*Q. mongolica*	China	**OM745992**	**OM746424**	**OM746589**	–
C. murrayanae	MICH301494	II, III	*P. murrayana*	USA	**OM745993**	**OM746425**	**OM746590**	**OM721416**
	MICH301496	II, III	*P. murrayana*	USA	**OM745994**	**OM746426**	**OM746591**	**OM721417**
C. myricae	MICH253485	II, III	*Myrica asplenifolia*	Canada	**OM745995**	**OM746427**	**OM746592**	**OM721418**
	MICH253505	II, III	*M. gale*	Canada	**OM745996**	**OM746428**	**OM746593**	**OM721419**
C. occidentale	MICH253479	II, III	*R. gandfalii*	USA	**OM745997**	**OM746429**	**OM746594**	**OM721420**
	MICH253477	II, III	*R. odoratum*	USA	**OM745998**	**OM746430**	**OM746595**	**OM721421**
	MICH253481	II, III	*R. aureum*	USA	**OM745999**	**OM746431**	**OM746596**	**OM721422**
	OMpM-1	0, I	*P. monophylla*	USA	–	L76507	–	–
C. orientale	HMAS242640	II, III	*Q. aquifolioides*	China	**OM745999**	**OM746432**	**OM746598**	**OM721423**
	HMAS242641	II, III	*Q. aquifolioides*	China	**OM746000**	MK208291	MK193820	**OM721424**
	HMAS242642	II, III	*Q. aquifolioides*	China	**OM746001**	**OM746433**	**OM746599**	**OM721425**

Table 1 Continued.

Species	**Specimen No.**^{a}	**Spore stage**	**Host**	**Country**	**GenBank Accession No.**^{a}			
					SSU	**ITS**	**LSU**	**CO3**
C. peridiatum	HMAS6746	II, III	*Q. variabilis*	China	**OM746002**	**OM746434**	**OM746600**	**OM721426**
	HMAS77666	II, III	*Q. liaotungensis*	China	**OM746003**	**OM746435**	**OM746601**	**OM721427**
	HMAS77667	II, III	*Q. liaotungensis*	China	**OM746004**	**OM746436**	**OM746602**	**OM721428**
	HMAS82417	II, III	*Q. mongolica*	China	**OM746005**	**OM746437**	**OM746603**	**OM721429**
	HMAS82418	II, III	*Q. mongolica*	China	**OM746006**	**OM746433**	**OM746599**	**OM721430**
	HMAS82717	II, III	*Q. glandulifera*	China	**OM746007**	MK208292	MK193817	**OM721431**
	HMAS242500	II, III	*Q. variabilis*	China	**OM746008**	**OM746438**	**OM746604**	**OM721432**
	HMAS242501	II, III	*Q. variabilis*	China	**OM746009**	**OM746439**	**OM746605**	**OM721433**
	HMAS45784	0, I	*P. densata*	China	**OM746010**	**OM746440**	**OM746606**	**OM721423**
	HMAS86824	II, III	*Pinus* sp.	Canada	**OM746011**	**OM746441**	**OM746607**	**OM721434**
	HMAS82719	II, III	*Pinus* sp.	Canada	**OM746012**	**OM746442**	**OM746608**	**OM721435**
	NYBG267052	II, III	*Pinus* sp.	USA	**OM746013**	**OM746443**	**OM746609**	**OM721436**
	NYBG267053	II, III	*P. strobus*	Canada	**OM746014**	MK208298	MK193829	**OM721437**
	NYBG267051	II, III	*R. nigrum*	USA	**OM746015**	MK208296	MK193828	**OM721438**
	NYBG267061	II, III	*Ribes* sp.	Canada	**OM746016**	**OM746444**	**OM746610**	**OM721439**
	NYBG267059	II, III	*Ribes* sp.	Canada	**OM746017**	**OM746445**	**OM746611**	**OM721440**
	NYBG267057	II, III	*Ribes* sp.	USA	**OM746018**	**OM746446**	**OM746612**	**OM721441**
	TSH-R14230	II, III	*Pedicularis* sp.	Japan	**OM746019**	**OM746447**	**OM746613**	**OM721442**
	HMAS38589	II, III	*R. mandschuricum*	China	**OM746020**	**OM746448**	**OM746614**	**OM721443**
	MICH278063	II, III	*Eupatorium odoratum*	Venezuela	**OM746021**	**OM746449**	**OM746615**	**OM721444**
	MICH278062	II, III	*E. subscandens*	Bolivia	**OM746022**	**OM746450**	**OM746616**	**OM721445**
C. pini	D21	II, III	*Bartsia alpina*	Finland	–	KU320169	–	–
	38A	II, III	*Melampyrum nemorosum*	Finland	–	AY566270	–	–
	Cclone 3	II, III	*Melampyrum* sp.	Finland	–	JF713709	–	–
	Crust 1	0, I	*P. sylvestris*	Finland	–	KJ959593	–	–
	Crust 2	0, I	*P. sylvestris*	Finland	–	KJ959594	–	–
	MD1	0, I	*P. sylvestris*	Italy	–	X83890	–	–
	SG3	0, I	*P. sylvestris*	Greece	–	X83907	–	–
	GREEK1	0, I	*P. sylvestris*	Greece	–	X83908	–	–
	ALTYRE2	0, I	*P. sylvestris*	UK	–	X83914	–	–
C. pyriforme	MICH253420	0, I	*P. contorta*	USA	**OM746023**	**OM746451**	**OM746617**	**OM721446**
	MICH253360	II, III	*Com. pallida*	USA	**OM746024**	**OM746452**	**OM746618**	**OM721447**

Table 1 Continued.

Species	**Specimen No.[a]**	**Spore stage**	**Host**	**Country**	**GenBank Accession No.[a]**			
					SSU	**ITS**	**LSU**	**CO3**
C. qinlingense	HMAS56423	II, III	*Q. aliena*	China	**OM746025**	**OM746453**	**OM746619**	**OM721448**
	HMAS74356	II, III	*Q. aliena*	China	**OM746026**	**OM746454**	**OM746620**	**OM721449**
C. quercuum	MICH253529	II, III	*Q. rubra*	Canada	**OM746027**	**OM746455**	**OM746621**	**OM721450**
	MICH253530	II, III	*Q. rubra*	Honduras	**OM746028**	**OM746456**	**OM746622**	**OM721451**
	MICH253424	II, III	*Q. rubra*	Canada	**OM746029**	**OM746457**	**OM746623**	**OM721452**
	FLAS-F-45180	II, III	*Q. borealis*	USA	**OM746030**	**OM746458**	**OM746624**	**OM721453**
	MICH253337	II, III	*Q. coccinea*	USA	**OM746031**	**OM746459**	**OM746625**	**OM721454**
	MICH253547	II, III	*Quercus* sp.	USA	**OM746032**	**OM746460**	**OM746626**	**OM721455**
	ISC395258	II, III	*Q. imbricaria*	USA	**OM746033**	**OM746461**	**OM746627**	**OM721456**
	CqE9WM-FP	0, I	*P. banksiana*	USA	–	JN943197	–	–
	CqE7WM-FP	0, I	*P. banksiana*	USA	–	JN943198	–	–
	MICH301230	0, I	*P. halepensis*	USA	**OM746034**	**OM746462**	**OM746628**	**OM721457**
	CcL-1	0, I	*P. leiophylla*	USA	–	L76486	–	–
	UBC-F5948	0, I	*P. sylvestris*	Canada	**OM746035**	**OM746463**	**OM746629**	**OM721458**
	CqfR4-FP	0, I	*P. taeda*	Canada	–	JN943193	–	–
	CqfD4-FP	0, I	*P. taeda*	USA	–	JN943196	–	–
	795CR-PNB-LI1	0, I	*Pinus* sp.	Canada	–	JN943229	–	–
	432PEH-PN-X21	0, I	*Pinus* sp.	Canada	–	JN943239	–	–
	428PEH-PN-QC13	0, I	*Pinus* sp.	Canada	–	JN943244	–	–
	424PEH-PN-MW1	0, I	*Pinus* sp.	Canada	–	JN943248	–	–
	40CR-PNB-LP1	0, I	*Pinus* sp.	Canada	–	JN943249	–	–
	TDB152	0, I	*Pinus* sp.	USA	–	AF522175	–	–
	CFB22250	0, I	*Pinus* sp.	USA	–	AY700193	–	–
	807-ISFSL-FP	0, I	*Pinus* sp.	USA	–	JN943191	–	–
	G-317-HGS1-FP	0, I	*Pinus* sp.	USA	–	JN943192	–	–
C. ribicola	ZP-R594	II, III	*R. nigrum*	China	**OM746036**	**OM746464**	**OM746630**	**OM721459**
	ZP-R524	II, III	*R. nigrum*	China	**OM746037**	**OM746465**	**OM746631**	**OM721460**
	ZP-R512	II, III	*R. nigrum*	China	**OM746038**	**OM746466**	**OM746632**	**OM721461**
	ZP-R492	II, III	*R. nigrum*	China	**OM746039**	**OM746467**	**OM746633**	**OM721462**
	ZP-R486	II, III	*R. nigrum*	China	**OM746040**	**OM746468**	**OM746634**	**OM721463**
	ZP-R464	II, III	*R. nigrum*	China	**OM746041**	**OM746469**	**OM746635**	**OM721464**
	ZP-R460	II, III	*R. nigrum*	China	**OM746042**	**OM746470**	**OM746636**	**OM721465**
	ZP-R453	II, III	*R. nigrum*	China	**OM746043**	**OM746471**	**OM746637**	**OM721466**

Table 1 Continued.

Species	**Specimen No.**[a]	**Spore stage**	**Host**	**Country**	**GenBank Accession No.**[a]			
					SSU	**ITS**	**LSU**	**CO3**
	ZP-R4	II, III	*R. nigrum*	China	**OM746044**	**OM746472**	**OM746638**	**OM721467**
	ZP-R363	II, III	*R. nigrum*	China	**OM746045**	**OM746473**	**OM746639**	**OM721468**
	ZP-R352	II, III	*R. nigrum*	China	**OM746046**	**OM746474**	**OM746640**	**OM721469**
	ZP-R347	II, III	*R. nigrum*	China	**OM746047**	**OM746475**	**OM746641**	**OM721470**
	ZP-R332	II, III	*R. nigrum*	China	**OM746048**	**OM746476**	**OM746642**	**OM721471**
	UBC-F5899	II, III	*R. nigrum*	Canada	**OM746049**	**OM746477**	**OM746643**	**OM721472**
	UBC-F5890	II, III	*R. nigrum*	Canada	**OM746050**	**OM746478**	**OM746644**	**OM721473**
	UBC-F5886	II, III	*R. bracteosum*	USA	**OM746051**	**OM746479**	**OM746645**	**OM721474**
	TSH-17009	II, III	*R. sativum*	Japan	**OM746052**	**OM746480**	**OM746646**	**OM721475**
	NYBG3106213	II, III	*R. nigrum*	Switzerland	**OM746053**	**OM746481**	**OM746647**	**OM721476**
	NYBG267058	II, III	*Ribes* sp.	Canada	**OM746054**	**OM746482**	**OM746648**	**OM721477**
	NYBG267056	II, III	*Ribes* sp.	Canada	**OM746055**	**OM746483**	**OM746649**	**OM721478**
	MICH253525	II, III	*R. nigrum*	Romania	**OM746056**	**OM746484**	**OM746650**	**OM721479**
	ISC428956	II, III	*R. missouriense*	USA	**OM746057**	**OM746485**	**OM746651**	**OM721480**
	ISC395271	II, III	*R. lobbii*	USA	**OM746058**	**OM746486**	**OM746652**	**OM721481**
	ISC391137	II, III	*R. nigrum*	USA	**OM746059**	**OM746487**	**OM746653**	**OM721482**
	ISC351969	II, III	*R. nigrum*	USA	**OM746060**	**OM746488**	**OM746654**	**OM721483**
	ISC343765	II, III	*R. nigrum*	USA	**OM746061**	**OM746489**	**OM746655**	**OM721484**
	HMAS52870	II, III	*R. nigrum*	China	**OM746062**	**OM746490**	**OM746656**	**OM721485**
	RM-77	II, III	*Castilleja applegatei*	USA	–	GU727731	–	–
	RM-54	II, III	*Cas. applegatei*	USA	–	GU727730	–	–
	U396	II, III	*Ribes* sp.	USA	–	DQ354560	–	–
	TDB27354	II, III	*Ribes* sp.	USA	–	AF522166	–	–
	E11	0, I	*P. cembra*	Finland	–	KU320184	–	–
	TSH-1094	II, III	*P. coronata*	Japan	**OM746063**	**OM746491**	**OM746657**	**OM721486**
	CrBf-5	0, I	*P. lambertiana*	USA	–	L76496	–	–
	UBC-F5879	0, I	*P. monticola*	Canada	**OM746064**	**OM746492**	**OM746658**	**OM721487**
	HMAS66843	II, III	*P. strobus*	Japan	**OM746065**	**OM746493**	**OM746659**	**OM721488**
	rust 17	0, I	*P. strobus*	Finland	–	KJ959609	–	–
	FLAS-F-45265	0, I	*P. palustris*	USA	**OM746066**	**OM746494**	**OM746660**	**OM721489**
	FLAS-F-07047	0, I	*P. strobus*	USA	**OM746067**	**OM746495**	**OM746661**	**OM721490**
	Ru29	0, I	*P. peuce*	Norway	–	DQ445908	–	–

Table 1 Continued.

Species	**Specimen No.**[a]	**Spore stage**	**Host**	**Country**	**GenBank Accession No.**[a]			
					SSU	**ITS**	**LSU**	**CO3**
	906CRR-PNS-SLZ	0, I	*Pinus* sp.	Canada	–	JN943228	–	–
	913CRR-PNS-SMW	0, I	*Pinus* sp.	Canada	–	JN943224	–	–
	Sib1-FP	0, I	*Pinus* sp.	Russia	–	JN943190	–	–
C. ribis-taedae	HMAS52871	II, III	*R. nigrum*	China	**OM746068**	**OM746496**	**OM746662**	**OM721491**
	HMAS172046	II, III	*R. nigrum*	China	**OM746069**	**OM746497**	**OM746663**	**OM721492**
	FLAS-F-16581	0, I	*P. taeda*	USA	**OM746070**	**OM746498**	**OM746664**	**OM721493**
C. strobilinum	U-434	II, III	*Q. alba*	USA	–	DQ185028	–	–
	U-432	II, III	*Q. muehlenbergii*	USA	–	DQ190732	–	–
	FLAS-F-53222	0, I	*P. taeda*	USA	**OM746071**	MK208285	MK193823	**OM721494**
	CSt-2	0, I	*P. elliotii*	USA	–	L76482	–	–
	807-ISFSL-FP	–	Host unknown	USA	–	JN943191	–	–
	G-317-HGS1-FP	–	Host unknown	USA	–	JN943192	–	–
***Cronartium* sp.**	HMAS40888	II, III	*R. aureum*	Germany	**OM746072**	–	**OM746665**	–
	HMAS49226	II, III	*R. aureum*	USA	**OM746073**	**OM746500**	**OM746666**	–
	HMAS41544	II, III	*Saussurea bullockii*	China	**OM746074**	**OM746501**	**OM746667**	**OM721495**
	1359CHL_PCS_BC	0, I	*Picea sitchensis*	Canada	–	GU049466	–	–
	NYBG36379	II, III	*Ribes* sp.	USA	**OM746075**	**OM746502**	–	**OM721496**
	HMAS244165	0, I	*P. taiwanensis*	China	**OM746076**	**OM746503**	–	**OM721497**
Crossopsora notata	MICH253650	II, III	*Byrsonima crassifolia*	Guatemala	**OM746077**	**OM746504**	–	**OM721498**
	MICH253651	II, III	*B. intermedia*	Brazil	**OM746078**	**OM746505**	–	**OM721499**
Didymopsora solani	CUP-MG-000445	II, III	*Solanum argenteum*	Brazil	**OM746079**	**OM746506**	–	**OM721500**
	MICH278173	II, III	*S. swartzianum*	Brazil	**OM746080**	**OM746507**	–	**OM721501**
Endoraecium falciforme	BRIP 57583	II, III	*Acacia falciformis*	Australia	NG_065048	NR_132079	NG_059231	KJ862439
Endoraecium tierneyi	BRIP 27071	II, III	*A. harpophylla*	Australia	NG_065052	NR_155088	NG_059235	KJ862450

*a: CUP: Plant Pathology Herbarium, Cornell University, Ithaca, New York, USA; FLAS: University of Florida Herbarium, Florida Museum of Natural History, Florida, USA; HKAS: Herbarium, Kunming Institute of Botany, CAS, China; HMAS: Mycological Herbarium of Institute of Microbiology, CAS, China; ISC:Ada Hayden Herbarium, Iowa State University, Iowa, USA; MICH: University of Michigan Herbarium, University of Michigan, Michigan, USA; NYBG: New York Botanical Garden, New York, USA; NYS: New York State Museum, New York, USA; TSH: Plant Pathology Herbarium, University of Tsukuba, Tsukuba, Japan; UBC: University of British Columbia Herbarium, British Columbia, Canada; ZP: Personal collections by Peng Zhao.

Roman numerals according to Cummins & Hiratsuka (1983, 2003): spermagonia/spermatia (0), aecia/aeciospores (I), uredinia/urediniospores (II), telia/teliospores (III), and basidia/basidiospore (IV). We applied the definitions of spore stage and morphological types in the whole life cycle based on Cummins & Hiratsuka (2003).

Results

To determine the species boundaries of *Cronartium*, the ML and Bayesian phylogenetic analyses were conducted based on a dataset containing 257 specimens on *Pinus* and eight angiosperm families, i.e., *Asclepiadaceae*, *Fagaceae*, *Gentianaceae*, *Myricaceae*, *Santalaceae*, *Saxifagaceae*, *Scrophulariaceae*, and *Paeoniaceae*. Amplicons generated for SSU, ITS, LSU, and CO3 were approximately 890, 570, 800, 410 bp, respectively. ML and Bayesian analyses of the combined dataset yielded comparable topologies with slight changes in poorly supported branches. The best ML tree is shown (Fig. 1A-D). Twenty-six *Cronartium* species were recognized from multi-locus phylogenies, morphological distinction in aecial and telial stages, host specificity, and geographic origins. Those lineages that match known species of *Cronartium* are listed or re-described, while several new names are proposed with complete descriptions for these new taxa. The connections between spermogonia/aecia and uredinia/telia of 27 *Cronartium* species were elucidated (Table 2).

Table 2 Host alternation of *Cronartium* species recognized in this study.

Species	**Host range**		**Countries where *Cronartium* species listed as quarantine pests**^{b}
	Aecial hosts	**Telial host**	
C. appalachianum	*P. virginiana*	*Buckleya distichophylla*	–
C. arizonicum	*P. jeffreyi*, *P. ponderosa*, *P. scopulorum*	*Castilleja integra*, *Cas. laxa*, *Cas. linariaefolia*, *Cas. minor*, *Cas. patriotica*	–
C. armandii	*P. armandii*, *P. corensis*	*R. griffithii*, *R. maximowiczii*, *R. orientale*	–
C. bethelii	*P. palustris*, *P. strobus*	*Q. emoryi*, *Q. mongolica*	–
C. castaneae	*P. ponderosa*	*Castanea mollissima*, *Castanea* sp.	–
C. coleosporioides	*P. contorta* var. *latifolia*, *P. pumila*	*Cas. angustifolia*, *Cas. californica*, *Cas. coccinea*, *Cas. douglasii*, *Cas. foliolosa*, *Cas. integra*, *Cas. integrifolia*, *Cas. latifolia*, *Cas. laxa*, *Cas. linariaefolia*, *Cas. martini*, *Cas. miniata*, *Cas. minor*, *Cas. occidentalis*, *Cas. patriotica*, *Cas. rhexifolia*, *Cas. septentrionalis*, *Cas. sessiliflora*, *Cas. suksdorfii*, *Cas. sulphurea*, *Cas. tenuiflora*, *Cas. wightii*, *Lamourouxia cordifolia*, *L. dependens*, *L. rhinanthifolia*, *Melampyrum lineare*, *Orthocarpus luteus*, *Pedicularis bracteosa*, *Pedicularis groenlandica*, *Pedicularis surrecta*	China, Colombia, Croatia, Madagascar, Morocco, South Korea, Tunisia, Ukraine, UK
C. comandrae	*P. banksiana*, *P. contorta* var. *latifolia*, *P. contorta* var. *murrayana*, *P. eldarica*, *P. ponderosa var. scopulorum*, *P. ponderosa*	*Com. pallida*, *Com. livida*, *Com. richardsiana*, *Com. umbellata*, *Com. umbellata var. pallida*, *Com. umbellata var. umbellata*	China, Colombia, Croatia, Ecuador, Madagascar, Morocco, South Korea, Tunisia, Ukraine, UK
C. comptoniae	*P. banksiana*	*Co. asplenitolia*, *Co. peregrina*	Croatia, Ecuador, Madagascar, Morocco,

Table 2 Continued.

Species	**Host range**		**Countries where *Cronartium* species listed as quarantine pests**[b]
	Aecial hosts	**Telial host**	
			South Korea, Tunisia, Ukraine, UK
C. flaccidum	*P. banksiana*, *P. griffithii*, *P. hwangshanensis*, *P. yunnanensis*	*Gentiana wardii*, *Gentiana yunnanensis*, *Pae. officinalis*, *Pae. lactiflora*, *Vincetoxicum hirundinaria*, *V. officinale*	Colombia, Venezuela
C. floridanum	*P. palustris*	–	–
C. fusiforme	*P. echinata*, *P. elliottii*, *P. massoniana*, *P. silvestris*, *P. taeda*	*Cyanchum nigrum*, *Q. emoryii*, *Q. fabri*, *Q. nigra*, *Q. palustris*, *Q. serrata*, *Q. variabilis*	China, Croatia, Madagascar, Morocco, South Korea, Tunisia, Ukraine
C. keteleeriae	*Keteleeria davidiana*, *K. evelyniana*	–	–
C. mongolicum	–[a]	*Q. mongolica*	–
C. murrayanae	*P. murrayana*	–	–
C. myricae	–	*M. asplenifolia*, *M. gale*	–
C. occidentale	*P. edulis*, *P. monophylla*	*R. aureum*, *R. cereum*, *R. gandfalii*, *R. odoratum*, *R. velmtiunm*	–
C. orientale	*P. hwangshanensis*, *P. densata*, *P. densiflora*, *P. thunbergii*	*Castanea crenata*, *Q. aliena*, *Q. acutissima*, *Q. aquifolioides*, *Q. crispula*, *Q. fabri*, *Q. glandulifera*, *Q. glauca*, *Q. liaotungensis*, *Q. spinosa*, *Q. semicaipifolia*, *Q. phellos*, *Q. rubra*, *Q. serrata*, *Q. sponosa*, *Q. variabilis*	–
C. peridiatum	–	*Eupatorium odoratum*, *E. subscandens*, *R. mandschuricum*, *R. nigrum*	–
C. pini	*P. rigida*, *P. sylvestris*	*Bartsia alpina*, *Melampyrum nemorosum*	Argentina
C. pyriforme	*P. contorta*	*Com. pallida*, *Com. umbellata*	–
C. qinlingense	–	*Q. aliena*	–
C. quercuum	*P. banksiana*, *P. clausa*, *P. contorta*, *P. halepensis*, *P. leiophylla*, *P. sylvestris*, *P. taeda*	*Q. alba*, *Q. agrifolia*, *Q. borealis*, *Q. borealis var. maxima*, *Q. chapmanii*, *Q. coccinea*, *Q. digitata*, *Q. falcata*, *Q. glandulifera*, *Q. hypoleuca*, *Q. marylandica*, *Q. rubra*, *Q. velutina*	Croatia, Georgia, Madagascar, Morocco, Russia, Tunisia, Ukraine, UK
C. ribicola	*P. albicaulis*, *P. coronata*, *P. monticola*, *P. strobus*	*Pedicularis yezoensis*, *R. bracteosum*, *R. glandulosum*, *R. missouriense*, *R. nigrum*, *R. odoratum*, *R. roezlii var. cruentum*, *R. sativum*	China, Ecuador, Madagascar, Malaysia, Morocco, USA
C. ribis-taedae	*P. caramels*, *P. echinata*, *P. taeda*	*R. nigrum*	–
C. sahoanum	*P. pumila*	–	–
C. strobilinum	*P. caribaea*, *P. elliottii var. densa*, *P. taeda*	*Q. alba*, *Q. geminata*, *Q. laurifolia*, *Q. minima*, *Q. myrtifolia*, *Q. minima*, *Q. virginiana*	–
C. yamabense	*P. pumila*	–	–

[a]: Dash line indicates no aecial and telial host or host is unknown.

[b]: Confirmed from the International Plant Protection Convention (IPPC) database (https://www.ippc.int/zh/countries/all/regulatedpests/).

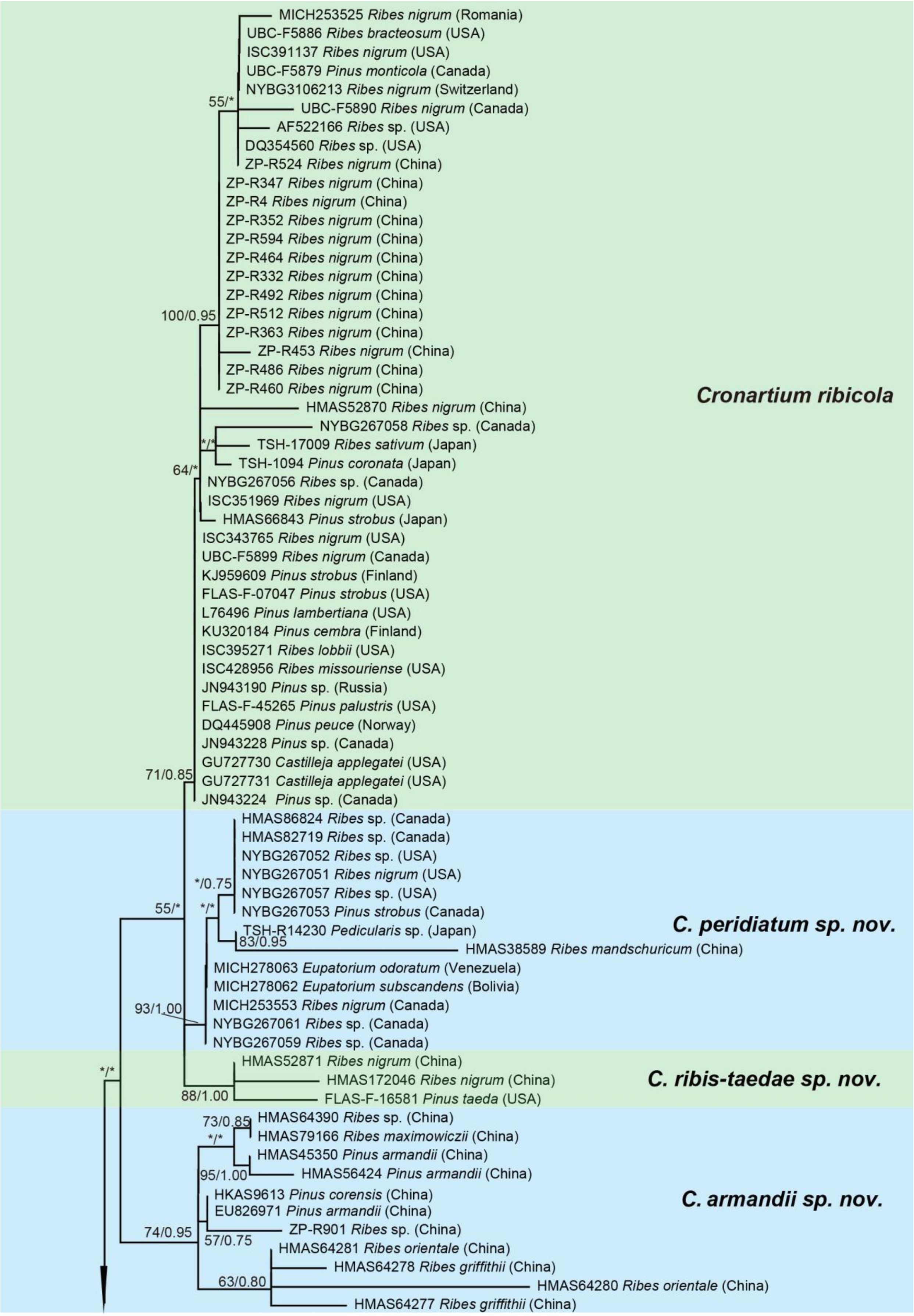

Figure 1A – Multilocus phylogenetic tree of the *Cronartium* species. One of the best trees was shown and the support values indicated at nodes. ML bootstrap ≤ 50% and BYPP ≤ 70% are indicated by dash line (–).

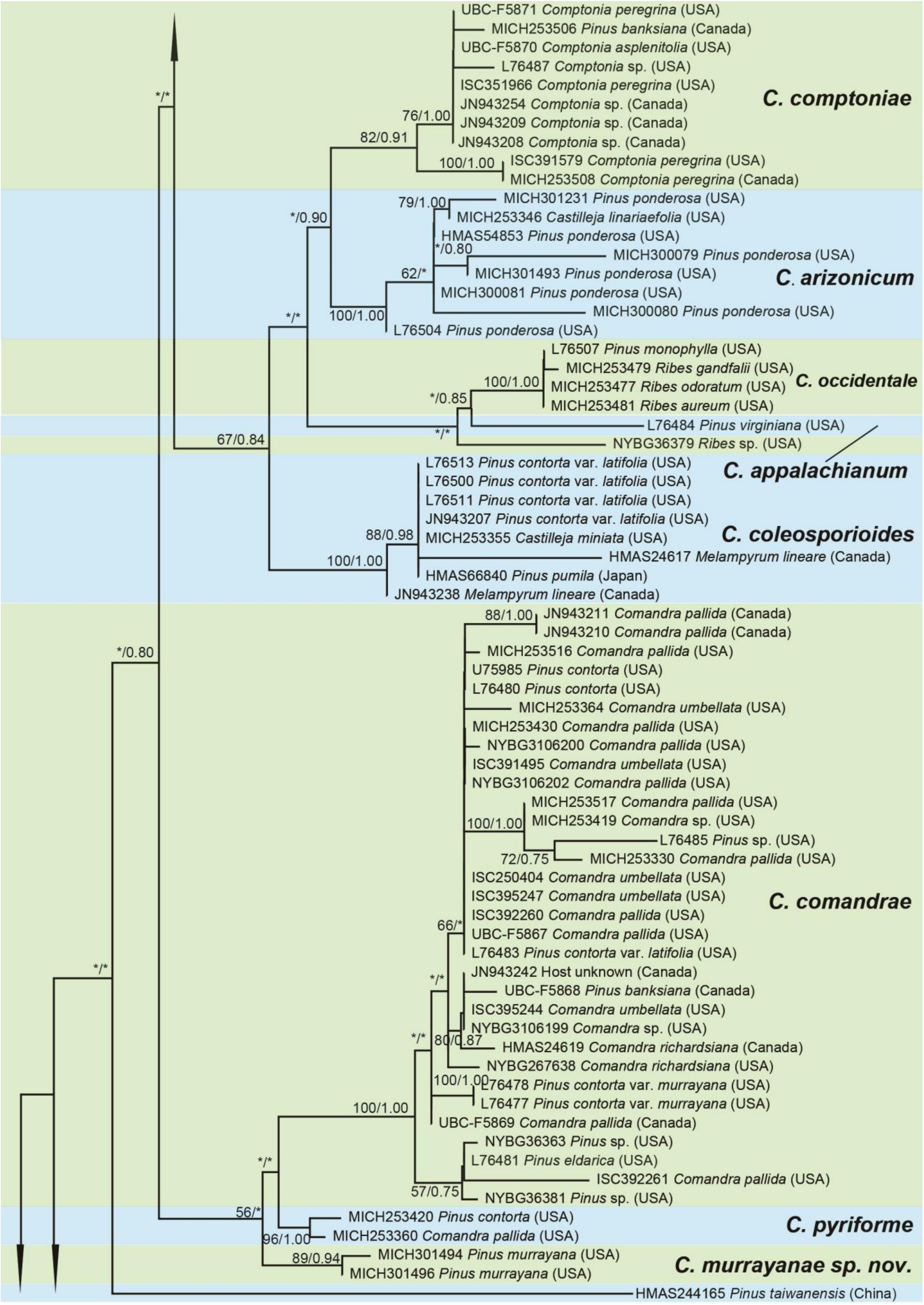

Figure 1B – Continued.

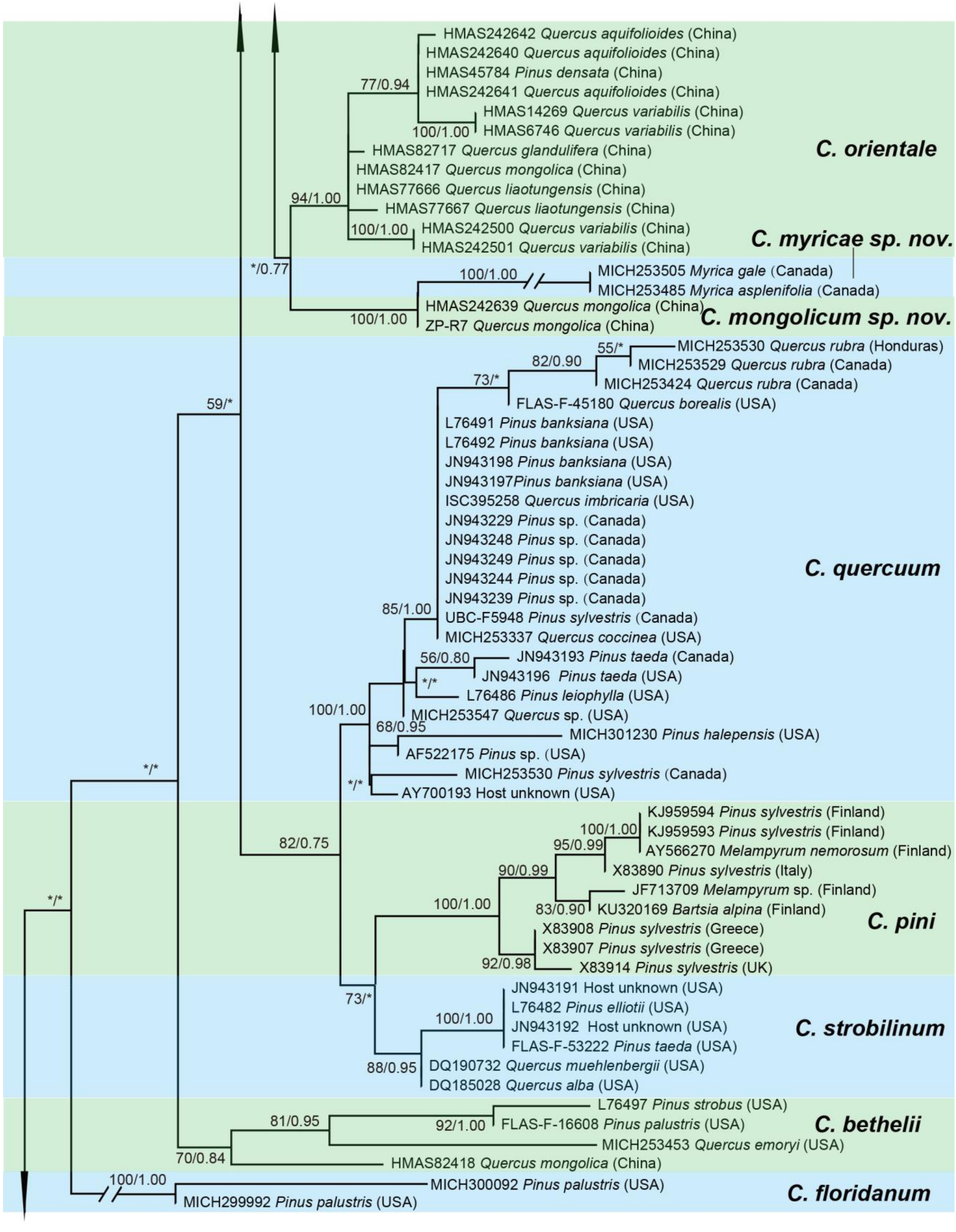

Figure 1C – Continued.

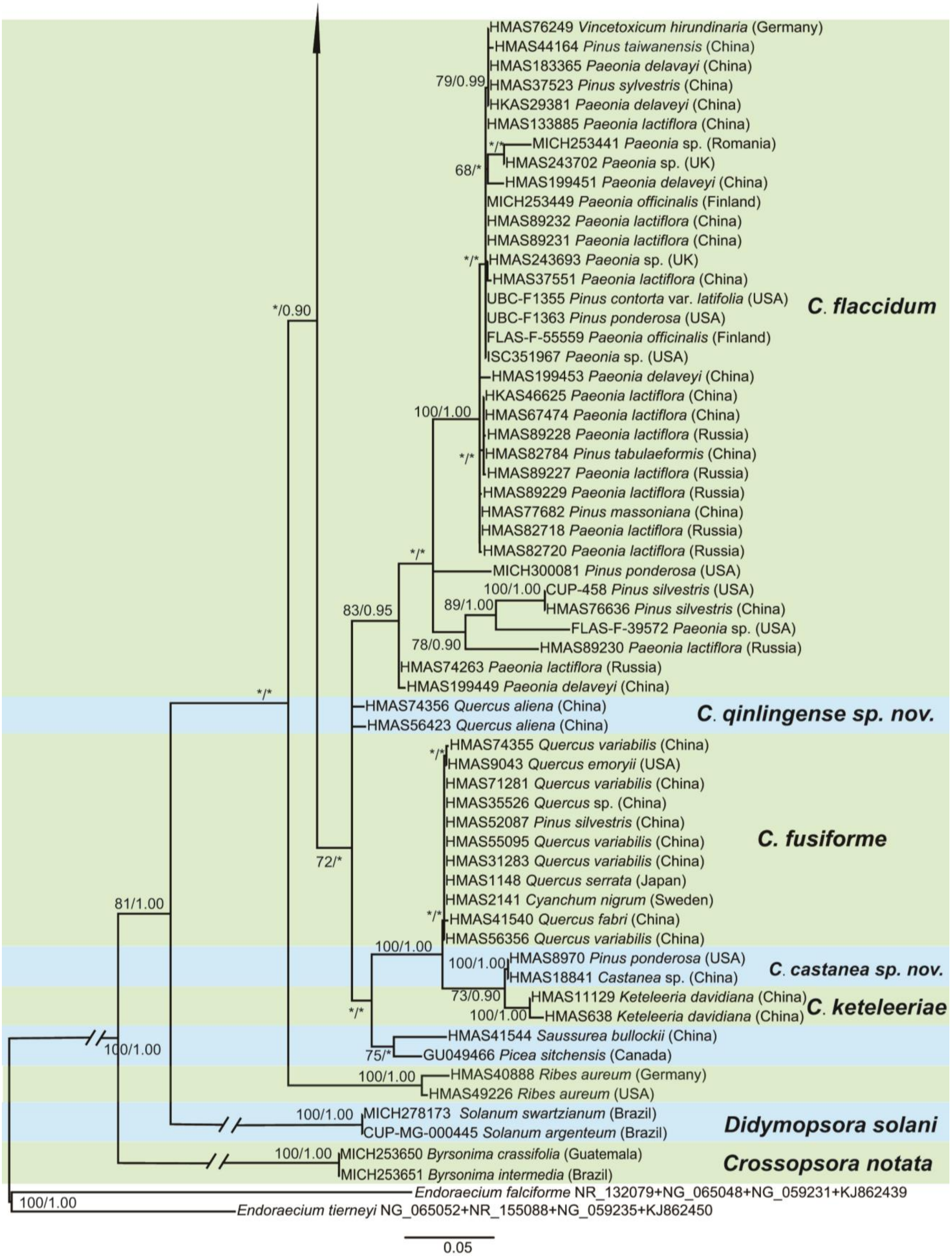

Figure 1D – Continued.

Taxonomy

Family: ***Cronartiaceae*** Dietel, in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1): 548. 1900.

MycoBank number: MB80659

Spermogonia Group II (type 9), intracortical, indeterminate, with flat hymenia, bounding structures lacking. Aecia *Peridermium*-type, the peridia large and blister-like, strongly developed, rupturing widely, aeciospores catenulate, with intercalary cells, verrucose with rod-like columns. Uredinia *Milesia*-type, subepidermal, opening by a pore, with ostiolar cells, urediniospores borne singly, echinulate, germ pores scattered. Telia with high variations, subepidermal, erumpent, teliospores aseptate, crowded but loosely adherent, some catenulate, thin-walled, germination occurs without dormancy. Basidia external.

Type genus – *Cronartium* Fr., Observ. Mycol. (Havniae) 1: 220. 1815.

Type species – *Cronartium asclepiadeum* (Willd.) Fr., Observ. Mycol. (Havniae) 1: 220. 1815.

***Cronartium* species recognized in this study:**

Cronartium appalachianum Hepting, Mycologia 49(6): 898. 1957.

MycoBank number: MB296132

Synonyms – *Peridermium appalachianum* Hepting & Cummins, Phytopathology 42: 115. 1952.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, peridia cylindrical, 3–7 mm high, peridial cells ellipsoid or oblong, 19–66 × 14–28 µm, wall verrucose, aeciospores ellipsoid, 16–34 × 12–23 µm, wall 2.0–5.0 µm thick, verrucose, warts annulate, 2–4 annuli. Uredinia hypophyllous, disperse or aggregate, urediniospores globose or ovoid, 18–25 × 11–16 µm, walls 1.0–2.0 µm, echinulate, germ pores scattered, 3–4. Telia hypophyllous or caulicolous, arising from the centre of uredinia, 0.5–1.5 mm long, yellowish or brown, columnar, cross-section of telia with 7–9 teliospores, teliospores oblong or cylindrical, 28–36 × 10–15 µm, wall 0.5–1.5 µm thick, hyaline.

Type – USA, Tennessee, II, III on *Buckleya distichophylla*, 11 Sept 1953, G.H. Hepting, PUR99777 (Isotype).

GenBank accession numbers – ITS: L76484.

Hosts and geographical distribution confirmed in this study – *Buckleya distichophylla* – USA; *P. virginiana* – USA.

Notes – Hepting & Cummins (1952) first described the rust fungus on *P. virginiana* in the USA as *Peridermium appalachianum*. Later, Hepting (1957) confirmed its telial host as *Buckleya distichophylla* (*Santalaceae*) through inoculation experiments and transferred it to the genus *Cronartium* based on telial morphology. *Cronartium appalachianum* is phylogenetically close to *C. occidentale* (Fig. 1B), but differs in the dimension of teliospores (28–36 × 10–15 µm vs 39–72 × 10–21 µm). Additionally, this species differs from other *Conartium* species in producing smaller urediniospores and aeciospores.

Cronartium arizonicum Cummins, Mycotaxon 20(2): 617. 1984. Fig. 2

MycoBank number: MB106742

Synonym – *Peridermium filamentosum* Peck, Bot. Gaz. 7(5): 56. 1882.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, peridia tubular, lacerated at apex or spreading, 4–7 mm high, peridial cells rhomboid, 22–85 × 18–33 µm, outer walls smooth, inner walls with small papillae, verrucose, wall hyaline, aeciospores oblong-ellipsoid, broadly ellipsoid, or oblong-pyriform, 22–32 × 13–21 µm, wall 1.5–3.0 µm, wall coarsely verrucose, hyaline, warts annulate, 3–5 annuli, variable in shape, cylindrical, or joined to form ridges or appearing labyrinthine, with small bumps on top. Uredinia hypophyllous, urediniospores obovate, broadly ellipsoid, 13–24 × 11–17 µm, wall 1.0 µm thick, echinulate, germ pores mostly scattered, inconspicuous. Telia with cornute columns, 0.4–1.2 mm long, straight, bright yellow, cross-section of telia with 8–12 teliospores, teliospores oblong, 30–70 × 9–19 µm, catenulate, wall brownish, with smooth surface, 0.4–1.1 µm thick, without surface ornamentation. Basidia external.

Type – USA, Arizona, II, III on *Cas. patriotica*, 10 Sept 1957, G.B. Cummins, PUR99777 (holotype).

Etypification – USA, Colorado, III on *Cas. linariaefolia*, 5 Sept 1914, E. Bartholomew, MICH253346 (epitype designated here, MBT10004989).

GenBank accession numbers from epitype – SSU: OM745897; ITS: MK208284; LSU: MK193824; CO3: OM721322.

Additional material examined – USA, Arizona, 0, I on *P. ponderosa*, 7 Jun 1935, H.E. Bailey, HMAS54853 & MICH301231; USA, California, 0, I on *P. ponderosa*, 14 May 1923, E. Bethel, HMAS8970; USA, California, 0, I on *P. jeffreyi*, 20 Jul 1920, E. Bethel, MICH300080; Colorado, 0, I on *P. scopulorum*, 12 Jun 1918, E. Bethel, MICH300079; USA, Idaho, 0, I on *P. ponderosa*, 20 Apr 1916, J.R. Weir, NYBG35870; USA, New Mexico, 0, I on *P. ponderosa*, 18 Jun 1917, E. Bethel, NYBG449424; USA, New Mexico, 0, I on *P. ponderosa*, 27 Jun 1957, G.B. Cummins, MICH301493.

Hosts range and geographical distribution confirmed in this study – *Cas. linariaefolia* – USA; *Cas. patriotica* – USA; *P. jeffreyi* – USA; *P. ponderosa* – USA; *P. scopulorum* – USA.

Additional host range and geographical distribution reported in previous studies – *Cas. integra* – USA; *Cas. laxa* – USA; *Cas. minor* – USA (Farr & Rossman 2021).

Notes – *Cronartium arizonicum* was discovered in Arizona, USA, and it has spermogonia/aecia on *P. ponderosa* and uredinia/telia on *Cas. patriotica* (Cummins 1984). In our phylogenetic tree (Fig. 1B), *C. arizonicum* was phylogenetically sister to *C. comptoniae*. Morphologically, it differs from *C. comptoniae* in the size of uredinia (13–24 × 11–17 µm vs 17–32 × 13–21 µm), the dimensions of teliospores (30–70 × 9–19 µm vs 32–55 × 6–17 µm) and the number of annuli on aeciospores (3–5 vs 4–6) (Fig. 2). We designated an epitype for this species and confirmed the host alternation on three *Pinus* and several *Castilleja* species (Table 2). This species is currently only known in North America.

Cronartium armandii X. Qi, P. Zhao & L. Cai; Mycosphere 12(1): 1143–1144. 2021. Fig. 3

MycoBank number: MB558588; Facesoffungi number: FoF 09996

Spermogonia not found. Aecia caulicolous, peridermioid, intracortical in origin, becoming erumpent, aeciospores borne singly, ellipsoid, obovoid, or subglobose, 10–13 × 6–11 µm, wall 2.0–3.0 µm, verrucae 1.4–2.5 µm high, densely verrucose, nailhead-like verrucae with 7–8 annuli, with obviously smooth area on surface, contents yellow. Uredinia usually lacked, urediniospores echinulate, sometimes with smooth surface at apex. Telia hypophyllous, hair-like columns, 0.4–1.0 µm long, straight or slight curved, bright yellow, teliospores oblong, cross-section of telia with 4–9 teliospores, 35–61 × 9–18 µm, catenulate, wall yellowish, brown, 0.4–0.9 µm thick, without surface ornamentation. Basidia external.

Type – China, Henan, Lushi, 0, I on *P. armandii*, May 1982, X.S. Li. HMAS45350 (holotype).

GenBank accession numbers from holotype – SSU: OM745911; ITS: MZ520620; LSU: MZ520623; CO3: OM721336.

Additional material examined – China. Shaanxi, Ningshan, 0, I on *P. armandii*, April 1966, J. Yao, HMAS56424; China, Gansu, Zhugqu, III on *R. maximowiczii*, Sept 1992, J.Y. Zhuang, HMAS79166; China, Tibet, Jilong, III on *R. orientale*, Sept 1990, J.Y. Zhuang, HMAS64281.

Host range and geographical distribution – *P. armandii* – China; *P. corensis* – China; *R. griffithii* – China; *R. maximowiczii* – China; *R. orientale* – China.

Notes – In China, two *Cronartium* species, i.e., *C. ribicola* and *C. quercuum*, have been found on *P. armandii* (Tai 1979). After detailed morphological and molecular examination of Chinese material, the rust fungus on *P. armandii* was identified as a novel species, *C. armandii* (Hyde et al. 2021). The life cycle is reported with aecial stage on *P. armandii* and telial stage on *R. maximowiczii* and *R. orientale* (Table 2). Based on morphological and molecular evidence, we confirmed the presence of *C. armandii* rather than *C. ribicola* on *P. armandii* in the southwest and central parts of China.

Figure 2 – Morphology of *Cronartium arizonicum*. a Caulicolous aecia erumpent from the bark. b Aecia with tubular peridia. c Aeciospores observed by LM. d Ultrastructure of aeciospores observed by SEM. e Aeciospores with nailhead-like verrucae with multiple layers. f Peridial cells observed by LM. g Inner walls of peridial cells with small papillae. h Label of epitype specimen. i Hair-like telia. j Columnar telia observed by SEM. k Telia with ostiolar cells. l Section of a telium observed by LM. m Ostiolar cells with smooth surface. Scale bars: c–d = 20 µm, e = 5 µm, f = 30 µm, g = 2 µm, j = 200 µm, k = 150 µm, l = 30 µm, m = 20 µm.


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Figure 3 – Morphology of *Cronartium armandii*. a Label of holotype specimen. b Caulicolous aecia on the bark of *P. armandii*. c Ellipsoid, obovoid, or subglobose aeciospores observed by LM. d Aeciospores observed by SEM. e Nailhead-like verrucae on surface of aeciospores. f Telia on the lower surface of *R. maximowiczi*i. g Hair-like telia; h. Section of a telium observed by LM. i Telia observed by SEM. j Smooth surface of teliospores observed by SEM. Scale bars: c–d = 10 µm, e = 2 µm, g = 500 µm, h = 50 µm, i = 100 µm, j = 50 µm.

Cronartium bethelii (Hedgc. & Long) Aime & Rossman, IMA Fungus 9(1): 81. 2018.

MycoBank number: MB824645

Basionym – *Peridermium bethelii* Hedgc. & Long [as ‘betheli’], Phytopathology 3(4): 251. 1913.

Spermogonia not found. Aecia caulicolous, not forming definite swellings, scattered, or confluent in small groups, peridia tubular, 2–6 mm high, peridial cells rounded, elliptical, oblong, or acuminate pyriform, 19–60 × 15–30 µm, outer walls smooth, inner walls irregularly compressed, with small papillae, verrucose, aeciospores oblong-ellipsoid, broadly ellipsoid, or oblong-pyriform, 25–48 × 15–25 µm, wall 3.0–4.0 µm, wall coarsely verrucose,warts annulate, 3–4 annuli, variable in shape, cylindrical, or joined to form ridges or appearing labyrinthine, with small bumps on top. Uredinia not found. Telia with cornute columns, 0.4–2.4 mm long, straight, bright yellow, cross-section of telia with 8–14 teliospores, teliospores oblong, 37–71 × 11–20 µm, catenulate, wall brownish, with smooth surface, 0.6–1.0 µm thick, without surface ornamentation.

GenBank accession numbers – SSU: OM745914; ITS: OM746353; LSU: OM746521; CO3: OM721339 (MICH253453).

Material examined – China, Heilongjiang, III on *Q. mongolica*, 28 Jul 2000, J.Y. Zhuang, HMAS82418; USA, Arizona, III on *Q. emoryi*, 2 Jul 1957, G.B. Cummins, MICH253453; USA, Florida, 0, I on *P. palustris*, 28 Feb 1919, G.G. Hedgcock, FLAS-F-16608.

Host range and geographical distribution – *P. palustris* – USA; *P. strobus* – USA; *Q. emoryi* – USA; *Q. mongolica* – China.

Notes – *Cronartium bethelii* has acuminate pyriform aeciospores and does not induce galls or significant hypertrophy on its host plants. Under the classification system emphasizing aecial morphologies (Peterson 1973, 1974), this fungus was previously classified as *Peridermium bethelii*, but recently transferred to *Cronartium* because Vogler & Bruns (1998) demonstrated that *Per. bethelii* was phylogenetically close to the members of *Cronartium*, particularly *C. comandrae*. Thus, Aime et al. (2018b) proposed a new combination, *C. bethelii*, with *Per. bethelii* as its basionym. Here we confirm the monophyly of this species (Fig. 1C), and recognize its telial hosts as two *Q.* species (Table 2).

Cronartium castaneae P. Zhao & L. Cai. sp. nov. Fig. 4

MycoBank number: MB842416; Facesoffungi number: FoF 12566

Etymology – refers to the host species on which the type specimen was collected.

Spermogonia not found. Aecia caulicolous, not forming definite swellings, mostly embedded in host tissue, peridia not found, aeciospores 25–33 × 14–22 µm, wall 2.0–3.5 µm, wall coarsely verrucose, warts annulate, 4–6 annuli. Uredinia not found. Telia with cornute columns, 0.5–1.5 mm long, straight, bright yellow, cross-section of telia with 6–9 teliospores, teliospores oblong, 33–56 × 14–22 µm, catenulate, wall brownish, 0.6–1.0 µm thick, without surface ornamentation. Basidia external.

Type – China, Nanjing, III on *Castanea* sp., 24 Jul 1922, B.N. Jiang & R.Y. Zheng, HMAS18841 (holotype).

GenBank accession numbers from holotype – SSU: OM745917; ITS: OM746356; LSU: OM746524; CO3: OM721342.

Additional material examined – China, Nanjing, III on *Castanea mollissima*, 8 Jun 1929, S.C. Teng, HMAS769; China, Nanjing, III on *Castanea* sp., 1 Dec 1954, B.N. Jiang & R.Y. Zheng, HMAS94221; China, Nanjing, III on *Castanea* sp., 1 Dec 1954, B.N. Jiang & R.Y. Zheng, HMAS94222; China, Nanjing, III on *Castanea* sp., 1 Dec 1954, B.N. Jiang & R.Y. Zheng, HMAS94223; USA, California, 0, I on *P. ponderosa*, 14 May 1923, E. Bethel, HMAS8970.

Hosts and geographical distribution confirmed in this study – *Castanea mollissima* – China; *Castanea* sp. – China; *P. ponderosa* – USA.

Notes – *Cronartium castaneae* is phylogenetically close to *C. keteleeriae* and *C. fusiforme* (Fig. 1D). Morphologically, it differs from *C. keteleeriae* in the size of aeciospores (25–33 × 14–22 µm vs 40–65 × 31–47 µm), the ornamentation of aeciospores, and the dimension of teliospores (33–56 × 14–22 µm vs 25–39 × 11–17 µm); from *C. fusiforme* in its aecia without peridia, and the dimension of aeciospores (25–33 × 14–22 µm vs 17–45 × 15–27 µm) (Fig. 4). *Cronartium orientale* and *C. quercuum* had previously been reported on *Castanea* species (Hirastuka et al. 1992, Kaneko 2000), but *C. castaneae* is phylogenetically distinct from these two species (Fig. 1B, D). *Cronartium castaneae* differs from *C. orientale* in aecia without peridia, dimension of aeciospores (25–33 × 14–22 µm vs 18–25 × 13–22 µm) and length of telia; from *C. quercuum* in its aecia without peridia, morphologies of uredinia. The telial hosts of two species are different.

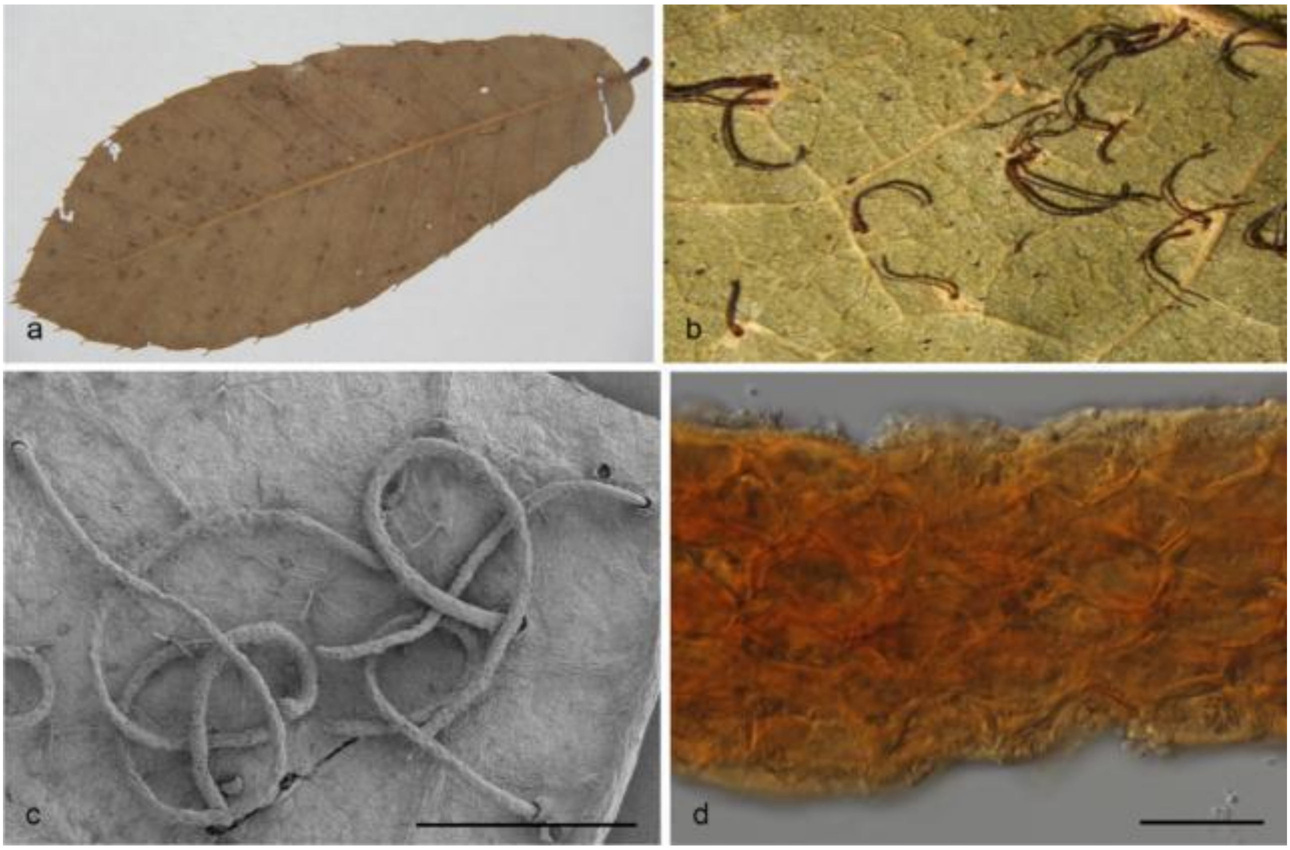

Figure 4 – Morphology of *Cronartium castaneae*. a-b Hair-like, hypophyllous telia on *Castaneae* species. c Columnar telia observed by SEM. d Section of a telium observed by LM. Scale bars: c = 300 µm, d = 30 µm.

Cronartium coleosporioides (Dietel & Holw.) Arthur, N. Am. Flora 7: 123. 1907.

MycoBank number: MB237984

Basionym – *Uredo coleosporioides* Dietel & Holw., Erythea 1: 247. 1893.

Synonyms – *Peridermium stalactiforme* Arthur & F. Kern, Bull. Torrey Bot. Club 33: 419. 1906.

Cronartium stalactiforme (Arthur & F. Kern) Arthur & F. Kern, Bull. Torrey Bot. Club 49: 191. 1922.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, peridia tubular, lacerating at apex or spreading, 4.0–7.0 mm high, peridial cells rhomboid, 52–88 × 15–22 µm, outer walls smooth, inner walls with small papillaes, side walls moderately verrucose, aeciospores broadly ellipsoid, oblong or globose, 21–32 × 11–22 µm, wall 1.5–3.0 µm, wall coarsely verrucose, warts annulate, 3–5 annuli, variable in shape, cylindrical, with small bumps on top. Uredinia hypophyllous or caulicolous, urediniospores obovate, broadly ellipsoid, 18–29 × 14–24 µm, wall 1.0–2.5 µm thick, echinulate, germ pores mostly scattered, inconspicuous. Telia hypophyllous or caulicolous, with cornuted columns, 0.1–1.0 mm long, straight, bright yellow, cross-section of telia with 9–13 teliospores, teliospores oblong, 30–66 × 11–16 µm, catenulate, wall brownish, with smooth surface, 0.7–1.3 µm thick, without surface ornamentation. Basidia external.

Type – USA, Washington, II, III on *Cas. miniata*, 10 Aug 1886, W.N. Suksdorf (lectotype designated here, NYBG69667).

GenBank accession numbers – ITS: L76500, L76511, L76513.

Additional material examined – Canada, III on *Melampyrum lineare*, 13 Aug 1957, J.A. Parmelee, HMAS24617; Honduras, Uyuca, III on *Cas. integrifolia*, 13 Jan 1951, A.S. Muller, FLAS-F-43533; Japan, Nagano, 0, I on *P. pumila*, 20 Jun 1989, M. Kakishima, HMAS66840; USA, Idaho, 0, I on *P. contorta* var. *latifolia*, 27 May 1917, J.R. Weir, NYBG3106198; USA, Washington, III on *Cas. minita*, 27 Jun 1934, G.G. Hedgcock, FLAS-F-45147.

Hosts range and geographical distribution confirmed in this study – *Cas. integrifolia* – Honduras; *Cas. miniata* – USA; *Melampyrum lineare* – Canada; *P. contorta* var. *latifolia* – USA; *P. pumila* – Japan.

Additional host range and geographical distribution reported in previous studies – *Cas. angustifolia* – Canada; *Cas. californica* – USA; *Cas. coccinea* – Canada; *Cas. douglasii* – USA; *Cas. foliolosa* – Canada; *Cas. integra* – USA; *Cas. latifolia* – USA; *Cas. laxa* – USA; *Cas. linariaefolia* – USA; *Cas. martini* – USA; *Cas. miniata* – Canada; *Cas. minor* – USA; *Cas. occidentalis* – Canada; *Cas. patriotica* – USA; *Cas. rhexifolia* – USA; *Cas. septentrionalis* – Canada; *Cas. sessiliflora* – Canada; *Cas. suksdorfii* – USA; *Cas. sulphurea* – USA; *Cas. tenuiflora* – Costa Rica; *Cas. wightii* – USA; *Lamourouxia cordifolia* – Guatemala; *Lamourouxia dependens* – Guatemala; *Lamourouxia rhinanthifolia* – Guatemala; *Melampyrum lineare* – USA; *Orthocarpus luteus* – Guatemala, South Dakota; *Pedicularis bracteosa* – Canada, USA; *Pedicularis groenlandica* – USA; *Pedicularis surrecta* – USA (Farr & Rossman 2021).

Notes – In the phylogenetic tree (Fig. 1B), *C. coleosporioides* formed a separate clade but sister to several timber rusts, i.e., *C. appalachianum*, *C. arizonicum*, *C. occidentale* and *C. comptoniae*. Morphologically it differs from *C. appalachianum* in the dimension of peridial cells (52–88 × 15–22 µm vs 19–66 × 14–28 µm), the number of annuli on aeciospores (3–5 vs 2–4), the number of teliospores in the cross-section of telia (9–13 vs 7–9), and the dimension of teliospores (30–66 × 11–16 µm vs 28–36 × 10–15 µm); from *C. arizonicum* in the dimension of peridial cells (52–88 × 15–22 µm vs 19–66 × 14–28 µm) and urediniospores (18–29 × 14–24 µm vs 13–24 × 11–17 µm); from *C. occidentale* in the dimension of peridial cells (52–88 × 15–22 µm vs 26–45 × 14–26 µm) and the dimension of teliospores (30–66 × 11–16 µm vs 39–83 × 10–21 µm); from *C. comptoniae* in the shape of peridial cells, the number of teliospores in cross-section of telia (9–13 vs 7–9) and the dimension of teliospores (30–66 × 11–16 µm vs 32–55 × 10–17 µm). Here, we confirmed the species boundaries, host alternation and geographic distribution of *C. coleosporioides*. Although this species was initially discovered on *Cas. foliolosa* in the USA (Arthur 1907), it is now distributed in a number of countries across the America continent (Farr & Rossman 2021). Due to the significant damage caused by this fungus to pine forest, more attention should be paid to determine the incidence of this important pathogen in Asian and European countries.

Cronartium comandrae Peck, Bot. Gaz. 4(2): 128. 1879. Fig. 5

MycoBank number: MB237307

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, peridial cells ellipsoid, globose or isodiametric, 22–37 × 15–29 µm, cell walls about 4–5 µm thick, verrucose, aeciospores oblong-pyriform, broadly ellipsoid, fusiform, with apparent tips at apex, 24–47 × 10–23 µm, wall verrucose, 0.5–2.5 µm thick, warts with 1 annulus, variable in shape. Uredinia always lacked. Telia amphigenous on leaves or caulicolous, yellowish or brown, columnar, 0.4–1.3 mm, cross-section of telia with 12–15 teliospores, teliospores ellipsoid or elongate, 28–43 × 12–19 µm, catenulate, wall 0.5–3.5 µm thick.

Type – USA, Colorado, III on *Com. pallida*, 11 Dec 1898, T.S. Brandegee, NYS-F-000815 (holotype).

Epitypification – USA, Colorado, III on *Com. pallida*, 7 Oct 1914, G.G. Hedgcock, UBC-F5867 (epitype designated here, MBT10004990).

Figure 5 – Morphology of *Cronartium comandrae*. a Caulicolous aecia erumpent from bark or trunks on pines. b Oblong-pyriform aeciospores observed by SEM. c Aeciospores with one annulus wart. d. Telia on the leaf and stem of *Com. Pallida*. e Columnar telia on leaf. f Telia observed by SEM. g A telium observed by LM. h Smooth surface of teliospores observed by SEM. i External basidium observed by LM. Scale bars: b = 10 µm, c = 5 µm, e = 1 mm, f = 100 µm, g = 30 µm, h = 10 µm, i = 30 µm.

GenBank accession numbers from epitype – SSU: OM745934; ITS: OM746370; LSU: OM746538; CO3: OM721359.

Additional material examined – Canada, Alberta, 0, I on *P. banksiana*, 10 Jun 1960, J.A. Baranyay, UBC-F5868; Canada, British Columbia, III on *Com. pallida*, 20 Jul 1948, B.M. Lawson & G.E. Woolliams, UBC-F5869; Canada, British Columbia, III on *Comandra* sp., 20 Jul 1956, J.A. Calder, NYBG3106203; Canada, British Columbia, III on *Comandra* sp., 27 Aug 1956, J.A. Calder, NYBG3106204; Canada, Manitoba, III on *Com. richardsiana*, 29 Jul 1949, S.M. Pady, NYBG267638; Canada, Manitoba, III on *Com. richardsiana*, 11 Aug 1955, J.A. Parmelee, HMAS24619; Canada, Ontario, III on *Comandra* sp., Jul 1910, J. Dearness, NYBG3106205; USA, California, 0, I on *P. contorta*, 1 Aug 1942, Lee Boner, FLAS-F-40604; Colorado, III on *Com. pallida*, 21 Aug 1897, J. B. Ellis, HMAS47711; USA, Colorado, III on *Comandra* sp., 21 Aug 1897, J.B. Ellis, HKAS39954; USA, Colorado, 0, I on *P. scopulorum*, Jun 1918, N.R. Hunt, NYBG36381; USA, Colorado, 0, I on *Pinus* sp., collector and date unknown, NYBG36363; USA, Colorado, 0, I on *P. ponderosa var. scopulorum*, 19 Jun 1912, G.G. Hedgcock & E. Bethel, UBC-F5866; USA, Illinois, III on *Com. umbellata*, 9 Sept 1889, M.B. Waite, ISC395244 (ISC-F-0068278); USA, Iowa, III on *Com. umbrellata*, 3 Sept 1983, L.H. Tiffany, ISC0431899 (ISC-F-79955); USA, Iowa, III on *Com. umbrellata*, 6 Aug 1886, R. Cratty, ISC0395242 (ISC-F-68274); USA, Iowa, III on *Com. umbellata*, 27 Jun 1986, L.H. Tiffany, ISC0431900 (ISC-F-79954); USA, Iowa, III on *Comandra* sp., May 1932, J.C. Gilman, ISC250404 (ISC-F-0079956); USA, Massachusetts, III on *Com. umbellata*, 3 Sept 1910, A.B. Seymour, ISC391495 (ISC-F-0068280); Michigan, 0, I on *P. banksiana*, 1 May 1917, C.K. Dodge, MICH253430; USA, Michigan, III on *Com. livida*, 19 Aug 1930, C.A. Brown, MICH253424; USA, Michigan, III on *Comandra* sp., 9 Aug 1914, E.B. Mains, MICH253419; USA, Montana, 0, I *P. ponderosa*, 20 Jun 1916, J.R. Weir, NYBG35392; USA, Montana, 0, I *P. ponderosa*, 8 Oct 1916, J.R. Weir, NYBG35874; USA, Montana, III on *Com. pallida*, date unknown, R.F.D. Kelsey, MICH253330; USA, Montana, III on *Comandra* sp.,10 Sept 1915, E.T. Bartholomew, NYBG3106200; USA, Montana, III on *Comandra* sp., 30 Jul 1916, J.R. Weir, NYBG3106202; USA, Montana, III on *Com. pallida*, 20 Jun 1916, J.R. Weir, NYBG35868; USA, Montana, III on *Comandra* sp., 18 Aug 1990, F.D. Kelsey, NYBG3106199; USA, Montana, III on *Comandra* sp., 8 Aug 1908, J. Clemens, NYBG3106201; USA, Montana, III on *Comandra* sp., 10 Sept 1915, E. Bartholomew, FLAS-F-07012; USA, Wisconsin, III on *Com. umbellata*, 2 Aug 1955, H.C. Greene, MICH253364; USA, Wisconsin, III on *Com. umbellata,* 27 Aug 1940, H.C. Greene, ISC395247 (ISC-F-0068282); USA, Wyoming, III on *Com. pallida*, Aug 1898, T.A. Williams, ISC0392260 (ISC-F-68277); USA, Wyoming, III on *Com. pallida*, 1 Aug 1926, A. Nelson, MICH253516; USA, Wyoming, III on *Com. pallida*, 20 Aug 1923, C.H. Kauffman, MICH253517; USA, Wyoming, III on *Com. pallida*, Aug 1897, Griffiths, ISC392261 (ISC-F-0068276); USA, Wyoming, III on *Com. pallida*, 21 Aug 1911, E. Bartholomew, FLAS-F-07013; USA, Wyoming, III on *Com. pallida*, Sept 1953, Parks, HKAS35399.

Hosts range and geographical distribution confirmed in this study – *Com. pallida* – Canada, USA; *Com. livida* – USA; *Com. richardsiana* – Canada, USA; *Com. umbellata* – Canada, USA; *P. banksiana* – Canada; *P. contorta* var. *latifolia* – USA; *P. contorta var. murrayana* – USA; *P. eldarica* – USA; *P. ponderosa* var. *scopulorum* – USA; *P. ponderosa* – USA.

Additional host range and geographical distribution reported in previous studies – *Com. livida* – Canada; *Com. umbellata var. pallida* – USA; *Com. umbellata var. umbellata* – USA (Farr & Rossman 2021).

Notes – *Cronartium comandrae* was initially described on *Com. pallida* in Colorado, USA, and its aecial host was discovered on *P. banksiana* (Peck 1879, Peterson 1973). Due to unsuccessful DNA extraction from the holotype specimen, we chose a similar specimen that was comparable in morphology, host, and location as an epitype. In the phylogenetic tree (Fig. 1B), *C. comadrae* formed a distinct clade sister to *C. pyriforme* and *C. murrayanae*. Morphologically, it differs from *C. pyriforme* in the dimension of aeciospores (24–47 × 10–23 µm vs 43–69 × 14–26 µm) and the annuli on aeciospores (1–2 vs 1); from *C. murrayanae* in the dimension of peridial cell

(22–37 × 15–29 µm vs 18–26 × 13–17 µm), the ornamentation of peridial cells, and the dimension of aeciospores (24–47 × 10–23 µm vs 29–62 × 11–22 µm); from other *Cronartium* species in its oblong-pyriform aeciospores with 1–2 annuli (Fig. 5). We confirmed its aecial hosts on *P. banksiana*, *P. contorta var. latifolia*, *P. contorta var. murrayana*, and *P. eldarica*, and telial hosts have been confirmed on several *Comandra* species and their varieties (Table 2).

Figure 6 – Morphology of *Cronartium comptoniae*. a Caulicolous aecia erumpent from bark or trunks on pines. b Oblong-ellipsoid, ovoid aeciospores observed by SEM. c Aeciospores with annulate warts. d Peridial cells observed by SEM. e Hypophyllous uredinia and telia. f Oval-

obovate urediniospores observed by LM. g Section of a telium observed by LM. h A telium observed by SEM. Scale bars: b = 20 µm, c = 2 µm, d = 50 µm, f = 20 µm, g–h = 50 µm.

Cronartium comptoniae Arthur, Bull. Torrey Bot. Club 33: 29. 1906. Fig. 6

MycoBank number: MB237767

Synonym – *Peridermium comptoniae* (Arthur) Orton & J.F. Adams, Phytopathology 4: 23. 1914.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, peridial cells isodiametric, 49–83 × 16–29 µm, verrucose wall hyaline, aeciospores oblong-ellipsoid, ovoid, 17–32 × 15–21 µm, wall 1.5–3.0 µm, wall coarsely verrucose, warts annulate, 4–6 annuli, variable in shape, cylindrical, or joined to form ridges or appearing labyrinthine, with small bumps on top. Uredinia hypophyllous, scattered or somewhat gregarious, 0.1 mm in diameter, with peridia in uredinia, cell polygonal and uniformly thin, 1 µm thick, and apparently thickened at apex, up to 10 µm, urediniospores oval-obovate, 19–33 × 16–22 µm, wall 2.5 µm thick, echinulate, germ pores scattered, inconspicuous. Telia hair-like columns, 0.7–2.0 mm long, straight or slight curved, bright yellow, cross-section of telia with 7–9 teliospores, teliospores oblong, 32–55 × 10–17 µm, catenulate, wall 0.5–1.3 µm thick, without surface ornamentation.

Type – USA, New Jersey, III on *Co. peregrina*, 7 Sept 1884, J.C. Arthur, PUR004393 (holotype).

Epitypification – USA, Connecticut, III on *Co. peregrina*, 15 Aug 1887, A.B. Seymour, ISC391579 (epitype designated here, MBT10004991).

GenBank accession numbers from epitype – SSU: OM745944; ITS: OM746380; LSU: OM746548; CO3: OM721369.

Additional material examined – Canada, Northwest Territories, 0, I on *P. banksiana*, 2 Jul 1949, W.J. Cody, MICH253506; Canada, Ontario, III on *Co. peregrina*, 6 Aug 1956, R.F. Cain, NYBG449416; USA, Connecticut, III on *Co. peregrina*, 15 Aug 1887, A.B. Seymour, ISC391579 (ISC-F-0068283); USA, Maine, III on *Co. peregrina*, 28 Jun 1949, J.T.B. Kingston, UBC-F5871; USA, Michigan, 0, I on *P. banksiana*, 1 Jun 1916, J.R. Weir, NYBG35873; Michigan, 0, I on *P. banksiana*, 1 Jun 1916, J.R. Weir, NYBG267640; USA, Minnesota, III on *Co. asplenitolia*, Aug 1923, E.E. Hubert, UBC-F5870; USA, New York, III on *Co. peregrina*, 2 Aug 1913, G.G. Hedgecock, NYBG449414; USA, New York, III on *Co. peregrina*, 17 Sept 1925, H.D. House, MICH253508.

Hosts range and geographical distribution confirmed in this study – *Co. asplenitolia* – Canada, USA; *Co. peregrina* – USA; *P. banksiana* – Canada, USA.

Notes – *Cronartium comptoniae* was first discovered on *Co. peregrina* (Arthur 1906). It is phylogenetically related to *C. arizonicum* (Fig. 1B), but the two species have different aecial and telial morphologies (see notes under *C. arizonicum*). Host alternation has been confirmed between two *Comptonia* species and *P. banksiana* (Table 2).

Cronartium flaccidum (Alb. & Schwein.) G. Winter, Hedwigia 19: 55. 1880.

MycoBank number: MB237708

Basionym – *Sphaeria flaccida* Alb. & Schwein., Consp. Fung. (Leipzig): 31. 1805.

Synonyms – *Cronartium paeoniae* Castagne, Cat. Pl. Mars.: 217. 1845.

Cronartium vincetoxici Duby, Bot. Gall., Edn 2 (Paris) 2: 909. 1830.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, 2.0–8.0 mm, peridia consisting of two cell layers, peridial cells almost isodiametric, 16–30 µm across, cell walls about 4–5 µm thick, verrucose, aeciospores rounded-ellipsoid or angular, 22–32 × 16–24 µm, walls 2.5–3.5 µm thick, verrucose, warts annulate, 4–6 annuli. Uredinia hypophyllous, gregarious, covered with hemispherical peridia, 0.5–2 µm long, urediniospores ovoid or ellipsoid, 18–30 × 15–20 µm, walls echinulate, germ pores scattered, inconspicuous. Telia arising from the centre of uredinia, yellowish or brown, columnar, 1.5–2.5 mm long, 55–140 µm wide, teliospores ellipsoid or elongate, cross-section of telia with 6–8 teliospores, 20–60 × 10–17 µm, wall 1–1.5 µm thick. Basidia external.

Material examined – Canada, British Columbia, 0, I on *P. contorta var. latifolia*, collector and date unknown, UBC-F1355; China, Anhui, 0, I on *P. hwangshanensis*, Sept 1989, H.S. Gao, HMAS79082; China, Heilongjiang, 0, I on *P. sylvestris*, Jun 1977, collector unknown, HMAS37523; China, Henan, 0, I on *P. taiwanensis*, May 1981, G.L. Ren, HMAS44164; China, Inner Mongolia, III on *Pae. lactiflora*, 20 Aug 1990, J.Y. Zhuang & S.X. Wei, HMAS67474; China, Inner Mongolia, III on *Pae. latiflora*, 22 Aug 1991, J.Y. Zhuang & S.X. Wei, HMAS74263; China, Inner Mongolia, III on *Pae. lactiflora*, 1 Aug 1990, J.Y. Zhuang & S.X. Wei, HMAS67475; China, Inner Mongolia, III on *Pae. lactiflora*, 22 Aug 1991, J.Y. Zhuang & S.X. Wei, HMAS74262; China, Inner Mongolia, III on *Pae. lactiflora*, 22 Aug 1991, J.Y. Zhuang & S.X. Wei, HMAS74263; China, Jilin, III on *Pae. lactiflora*, 20 Aug 2003, J.Y. Zhuang, HMAS89231; China, Liaoning, III on *Pae. lactiflora*, Aug 1975, B.Q. Tong, HMAS37551; China, Sichuan, 0, I on *P. sylvestris*, 23 Apr 1959, collector unknown, HMAS30623; China, Sichuan, III on *Pae. lactiflora*, 28 May 1979, Z.Y. Zhang, HMAS133885; Tibet, III on *Paeonia* sp., 29 Jun 1973, M. Zang, HKAS5009; China, Yunnan, III on *Pae. delavayi*, 20 Sept 2007, J.Y. Zhuang, HMAS199449; China, Yunnan, III on *Pae. delavayi*, 20 Sept 2007, J.Y. Zhuang, HMAS199453; China, Yunnan, III on *Pae. delavayi*, 20 Sept 2007, J.Y. Zhuang, HMAS199451; China, Yunnan, III on *Pae. delavayi*, 20 Sept 2007, J.Y. Zhuang, HMAS183365; China, Yunnan, III on *Pae. delavayi*, 31 Jul 1995, G. Durrieu, HKAS29381; China, Yunnan, III on *Pae. delavayi*, 2 Aug 1995, G. Durrieu, HKAS29581; Yunnan, III on *Pae. delavayi*, 2 Aug 1995, G. Durrieu, HKAS29582; Yunnan, III on *Pae. delavayi*, 4 Aug 1995, G. Durrieu, HKAS29609; Finland, Ålands skärgård, II, III on *Pae. officinalis*, 19 Sept 1942, Lauri E. Kari, FLAS-F-55559; Finland, Alands skärgård, III on *Pae. officinalis*, 21 Aug 1949, I. Kukkonen, MICH253449; Germany, Bayern, III on *Vincetoxicum hirundinaria*, 1 Aug 1993, D. Triebel & G. Rambold, HMAS76249; Germany, Brandenburg, III on *Vincetoxicum officinale*, 7 Sept 1932, H. Sydow, HMAS1144; Romania, III on *Paeonia* sp., 10 Aug 1948, T. Svulescu, MICH253441; Japan, Tottori, III on *Vincetoxicum officinale*, 7 Sept 1932, H. Sydow, HMAS1148; Russia, Khanka, III on *Pae. obovata*, 9 Aug 2003, J.Y. Zhuang, HMAS89230; Russia, Ussuriysk, III on *Pae. lactiflora*, 4 Aug 2003, J.Y. Zhuang, HMAS89229; Russia, Vladivostok, III on *Pae. lactiflora*, 3 Aug 2003, J.Y. Zhuang, HMAS89228; UK, Surrey, III on *Paeonia* sp., 4 Aug 2000, Royal Hort. Soc, Wisley, HMAS243693 & HMAS243702; USA, Arizona, 0, I on *P. ponderosa*, 4 Jul 1952, F.G. Hawksworth, UBC-F1363; USA, South Dakota, III on *Cas. sulphurea*, 8 Aug 1929, F.J. Seaver, ISC351967 (ISC-F-0068269); USA, Utah, III on *Paeonia* sp., 3 Sept 1944, A.S. Rhoads, FLAS-F-39572.

GenBank accession numbers – SSU: OM745947; ITS: OM746383; LSU: OM746551; CO3: OM721372 (FLAS-F-55559).

Hosts range and geographical distribution confirmed in this study – *Gentiana wardii* – China; *Gentiana yunnanensis* – China; *Pae. officinalis* – German; *Pae. lactiflora* – China; *P. banksiana* – Canada; *P. griffithii* – China; *P. hwangshanensis* – China; *P. yunnanensis* – China; *Vincetoxicum hirundinaria* – German; *Vincetoxicum officinale* – German, Japan.

Notes – *Cronartium flaccidum* was first reported on *Pae. officinalis* in Silesia region adjacent to Germany (Albertini & Schweinitz 1805). This species can be found throughout Eurasia and North America. Previously, Kasanen (1997), Kaitera et al. (1999, 2011, 2012), and Hantula et al. (2002) recognized the European rust fungus on *Bartsia* and *Melampyrum* as *C. flaccidum*, but we confirmed its identity as *C. pini*, which agreed with that of Wijesinghe et al. (2019). Two species were phylogenetically distinct and can be distinguished in the dimension of teliospores and the length of telia. Furthermore, the two species have different telial hosts. In the phylogenetic tree (Fig. 1D), *C. flaccidum* was closely related to *C. qinlingense*. Morphologically, the two species differ in the number of teliospores in the cross-section of telia (6–8 vs 3–5) and the dimension of teliospores (20–60 × 10–17 µm vs 20–47 × 7–23 µm).

Cronartium floridanum (Hedgc. & G. Hahn) P. Zhao & L. Cai. comb. nov.

MycoBank number: MB842418; Facesoffungi number: FoF 12567

Basionym – *Peridermium floridanum* Hedgc. & G. Hahn, Mycologia 12(4): 194. 1920.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, 1.0–4.5 mm long, peridia flattened laterally, rupturing longitudinally at the apex, peridial cells ellipsoid, ovoid, rhomboid, 31–74 × 16–34 µm, cell walls about 4–8 µm thick, verrucose, aeciospores ellipsoid or obovoid, 18–38 × 10–23 µm, walls 1.5–4 µm thick, most of their surface verrucose, warts annulate, 1–2 annuli, cylindrical. Uredinia and telia not found.

Material examined – USA, Florida, 0, I on *P. palustris*, 6 Nov 1896, P.H. Rolfs, FLAS-F-05303; USA, Florida, 0, I on *P. palustris*, date and collector unknown, FLAS-F-04914; USA, Florida, 0, I on *P. palustris*, date unknown, S.M. Tracy, MICH300092; USA, Florida, 0, I on *P. palustris*, date unknown, G.G. Hedgcock, MICH299992.

GenBank accession numbers – SSU: OM745976; ITS: OM746408; LSU: OM746576; CO3: OM721401 (MICH299992).

Hosts range and geographical distribution confirmed in this study – *P. palustris* – USA.

Notes – *Cronartium floridanum* was first reported (as *Per. floridanum*) on *P. palustris* in Florida, USA (Hedgcock et al. 1920). In this study, several specimens of *P. palustris* fitted well with the morphological description of *Per. floridanum*, and they clustered together within *Cronartium* clade (Fig. 1C). Our phylogenetic results confirmed *Per. floridanum* to be a member of *Cronartium*, thus we propose the new combination.

To date, three *Cronartium* species (i.e., *C. cerebrum*, *C. quercuum*, *C. strobilinum*) have been reported on *P. palustris* (Hiratsuka 1995). *Cronartium floridanum* differs from *C. cerebrum* in the length of the peridial cell (31–74 µm vs 35–50 µm, Peterson 1967) and the dimension of aeciospores (18–38 × 10–23 µm vs 26–28 × 17–20 µm, Peterson 1967); from *C. quercuum* in shape and dimension of peridial cells (31–74 × 16–34 µm vs 32–57 × 12–22 µm); from *C. strobilinum* in the dimension of peridial cells (31–74 × 16–34 µm vs 21–52 × 11–23 µm) and the shape of aeciospores.

Cronartium fusiforme Hedgc. & N.R. Hunt ex Cummins, Mycologia 48: 603. 1956.

MycoBank number: MB296133

Synonyms – *Peridermium fusiforme* Arthur & F. Kern, Bull. Torrey Bot. Club 33: 421. 1906.

Cronartium fusiforme Peck ex Hedgc. & N.R. Hunt, Phytopathology 8: 316. 1918. Nom. Nud.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, usually with spindle-shaped galls, peridial cells ellipsoid or linear, 58–117 × 15–27 µm, wall verrucose, aeciospores ellipsoid, oblong, or fusoid, 17–45 × 15–27 µm, wall 1.5–3.0 µm, wall coarsely verrucose, warts annulate, 1–2 annuli, variable in shape, cylindrical, or joined to form ridges or appearing labyrinthine, with small bumps on top. Uredinia hypophyllous, scattered, 0.2–0.4 mm in diameter, with paraphyses in uredinia, urediniospores oval, broadly ellipsoid, obovate, 19–33 × 16–22 µm, wall hyaline, 1.5–2.5 µm thick, echinulate, germ pores mostly scattered, inconspicuous. Telia hypophyllous, with hair-like columns, 1.2–3.5 mm long, straight or slight curved, bright yellow, cross-section of telia with 7–10 teliospores, teliospores oblong, 27–52 × 10–21 µm, catenulate, wall colorless, 2.5–5.5 µm thick, without surface ornamentation.

Type – USA, Florida, III on *Q. nigra*, 23 March 1914, W.H. Long, BPI032973 (holotype).

Material examined – China, Chongqing, III on *Q. variabilis*, 10 Aug 1994, N. Zhang, HMAS71281; China, Fujian, III on *Q. fabri*, 25 Oct 1980, J.Y. Zhuang, HMAS41540; China, Guizhou, III on *Quercus* sp., collector and date unknown, B.F. Hu, HMAS35526; China, Hainan, III on *Q. variabilis*, 13 Jun 1960, J.H. Yu & R. Liu, HMAS55095; China, Jiangsu, III on *Quercus* sp., 6 Oct 1958, Y.N. Yu, HMAS31283; China, Shaanxi, III on *Q. variabilis*, 19 Sept 1991, J.Y. Zhuang & S.X. Wei, HMAS74355; China, Shaanxi, III on *Q. variabilis*, date unknown, J.Y. Li & T.Y. Zhang, HMAS56356; Finland, 0, I on *P. silvestris*, 2 Jul 1965, T. Ulvinen, HMAS52087; Sweden, Upsala, III on *Cyanchum nigrum*, 19 Sept 1992, collector unknown, HMAS2141; USA, Arizona, III on *Q. emoryii*, 27 May 1922, E. Bethel, HMAS9043; USA, Columbia, III on *Q. palustris*, 24 May 1930, G.G. Hedgecock, NYBG449421; USA, Louisiana, III on *Quercus* sp., 5

Jun 1976, R.D. Goos, NYBG985620; USA, Louisiana, III on *Quercus* sp., 5 Jun 1976, R.D. Goos, NYBG985619.

GenBank accession numbers – SSU: OM745986; ITS: OM746418; LSU: OM746586; CO3: OM721411 (HMAS9043).

Hosts range and geographical distribution confirmed in this study – *Cyanchum nigrum* – Sweden; *P. massoniana* – China; *P. silvestris* – China; *Q. emoryii* – China, USA; *Q. fabri* – China, USA; *Q. nigra* – USA; *Q. palustris* – USA; *Q. serrata* – Japan; *Q. variabilis* – China; *Quercus* sp. –China, USA.

Additional host range and geographical distribution reported in previous studies – *P. echinata* – USA; *P. elliottii* – USA; *P. taeda* – USA (Farr & Rossman 2021).

Notes – *Cronartium fusiforme* was originally reported on the basis of the rust fungus on *Q. nigra* in Florida, USA, but this species was not validly published in the original literature due to lack of a morphological description (Hedgcock & Hunt 1918). Inoculation tests by Hedgcock & Siggers (1949) revealed the host alternation of this species. Based on the life cycle information, Cummins (1956) introduced the name *C. fusiforme* with a description that included both aecial and telial stages. Later this species was considered a synonym of *C. quercuum* (Burdsall & Snow 1977). It was once thought to be a race of *C. quercuum*, i.e., *C. quercuum* f. sp. *fusiforme* (Hiratsuka 1995). In our phylogenetic tree (Fig. 1C, D), *C. fusiforme* formed a well-supported clade distant from *C. quercuum*. Morphologically, it differs from *C. quercuum* in aecial morphology (spindle-shaped aecial gall vs globose-shaped aecial gall), uredinia with paraphyses, dimension of aeciospores (17–45 × 15–27 µm vs 23–33 × 16–23 µm), shape and dimension of peridial cells (58–117 × 15–27 µm vs 32–57 × 12–22 µm). *C. fusiforme* is listed as an important quarantine pathogen by the EU and Asian countries (Duan et al. 2017, EPPO 2021).

Cronartium keteleeriae F.L. Tai, Farlowia 3(1): 96. 1947. Fig. 7

MycoBank number: MB085865

Synonyms – *Chrysomyxa keteleeriae* (F.L. Tai) Y.C. Wang & R.S. Peterson, Acta Mycol. Sin. 1(1): 16. 1982.

Peridermium kunmingense W. Jen, J. Yunnan Univ., Nat. Sci. Ed.: 157. 1956.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, with fusiform shape, up to 10 cm, peridia tubular, spreading or erect, 3.0–13.5 mm high, peridial cells rhomboid-oblong, ellipsoid or linear, 36–67 × 18–32 µm, wall smooth, aeciospores ellipsoid, oblong, or fusoid, 40–65 × 31–47 µm, wall 1.5–4.0 µm, wall echinulate, with pits. Uredinia absent. Telia foliicolous, hypophyllous, scattered or aggregated, yellowish or brown, columnar, 2.5–6.5 mm long, 250–650 µm wide, teliospores rhomboid or oblong, 25–39 × 11–17 µm, wall 1.5–2.5 µm thick. Basidia external.

Type – China, Yunnan, Kunming, III on *Keteleeria evelyniana*, C.C. Cheo, HMAS638 (holotype).

GenBank accession numbers from holotype – SSU: OM745990; ITS: OM746422; CO3: OM721415.

Additional material examined – China, Yunnan, Kunming, III on *Keteleeria evelyniana*, 29 Jun 1938, C.C. Cheo & S.Z. Zhao, HMAS429 (paratype); China, Yunnan, Kunming, III on *Keteleeria evelyniana*, 30 Jun 1927, C.C. Cheo & S.Z. Zhao, HMAS13335; China, Yunnan, Kunming, III on *Keteleeria evelyniana*, 27 Jun 1980, K.G. Cao, HMAS40856; China, Yunnan, Kunming, III on *Keteleeria evelyniana*, 14 Jul 1980, K.Q. Kang, HMAS40558; China, Yunnan, Kunming, III on *Keteleeria evelyniana*, 14 Jul 1980, M. Zang, HKAS6088; China, Yunnan, Kunming, III on *Keteleeria evelyniana*, 6 Jul 1938, X. Ren, HMAS639; China, Yunnan, Kunming, III on *Keteleeria davidiana*, 20 Jun 1943, W.F. Chiu, HMAS11129; China, Yunnan, Kunming, III on *Keteleeria evelyniana*, 5 Jul 1945, W.N. Xiang & G.Z. Jiang, HMAS17620; China, Yunnan, Kunming, III on *Keteleeria evelyniana*, 14 Jul 1980, S.F. Sheng, HMAS45876 & HMAS45877.

Hosts and geographical distribution confirmed in this study – *Keteleeria davidiana* – China; *Keteleeria evelyniana* – China.

Notes – *Cronartium keteleeriae* was described by Tai (1947) on *Keteleeria* species in Yunnan province, China. Later, it was renamed *Chrysomyxa keteleeriae* (Ren et al. 1957, Wang & Peterson 1982). We were able to generated sequence data from the type material (HMAS638), elucidating that this species is phylogenetically close to *C. fusiforme* (Fig. 1D). As a result, the name *C. keteleeriae* is resurrected. Ren et al. (1992) reported its host alternation under the name of *Per. kunmingense*. It has an automicrocyclic life cycle with distinct morphological characteristics, i.e., fusiform aecia, large aeciospores, echinulate spines with pits, peridial cells with smooth surface, foliicolous telia, and relatively small teliospores (Fig. 7).

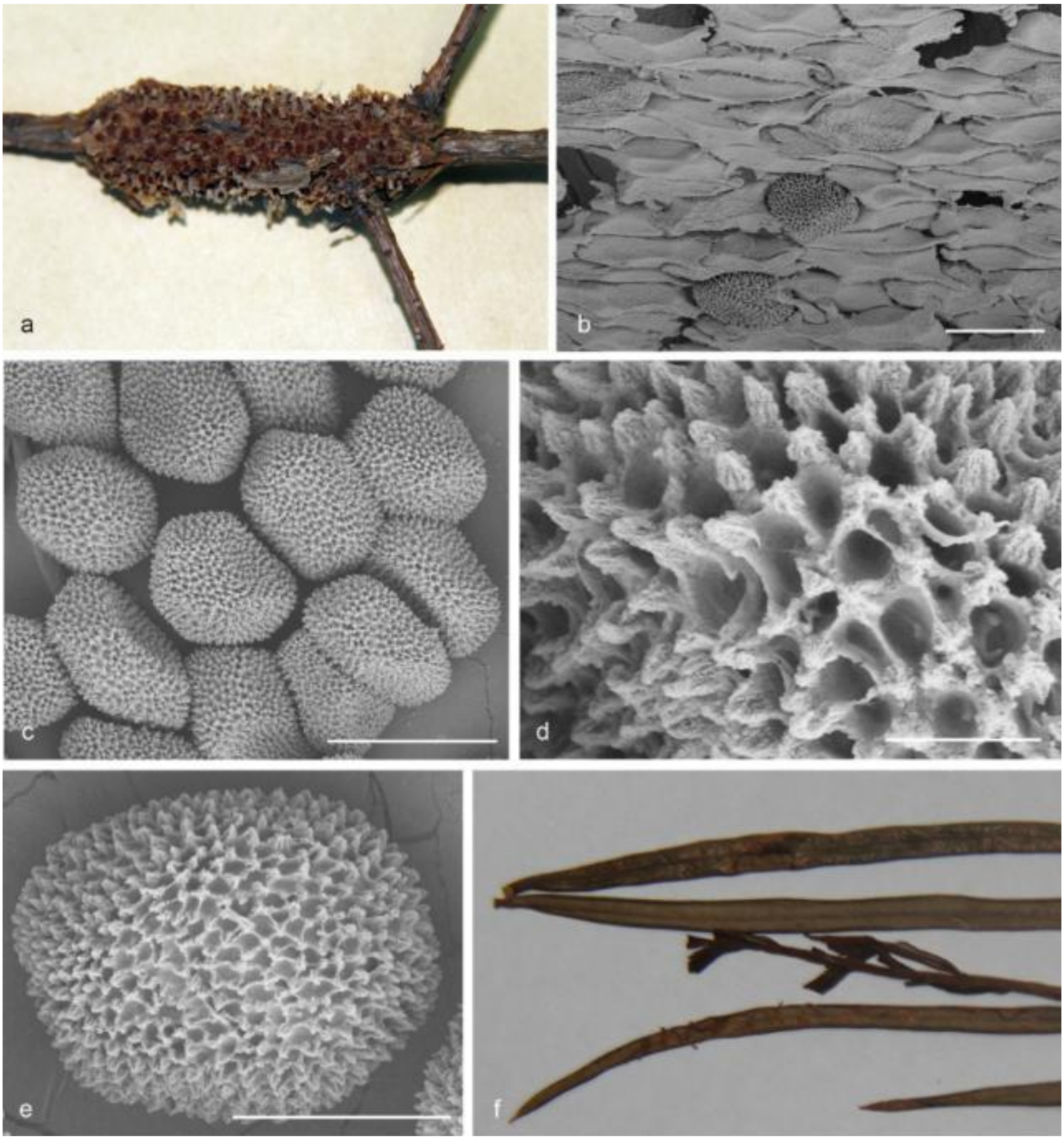

Figure 7 – Morphology of *Cronartium keteleeriae*. a Caulicolous aecia erumpent from trunk of *Keteleeria evelyniana*. b Peridial cells observed by SEM. c Ellipsoid, oblong, or fusoid aeciospores observed by SEM. d Ornamentation of aeciospores. e Aeciospore with pits on surface. f Hypophyllous telia on *Keteleeria* species. Scale bars: b–c = 50 µm, d = 2 µm, e = 20 µm.

Cronartium mongolicum P. Zhao & L. Cai, sp. nov. Fig. 8

MycoBank number: MB842419; Facesoffungi number: FoF 12568

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

Spermogonia and aecia unknown. Uredinia hypophyllous, scattered, 0.25–0.40 mm, yellow, with intra-uredinial paraphyses, urediniospores obovoid or ellipsoid, 16–25 × 12–19 µm, wall hyaline, 1.0–2.0 µm thick, echinulate. Telia hypophyllous, scattered, forming fusiform columns, straight or slightly curved, 4.0–21.5 mm long, brown, cross-section of telia with 6–9 teliospores, teliospores oblong or ellipsoid, 38–71 × 13–22 µm, wall yellowish brown, smooth, 0.4–1.2 µm. Basidia external.

Type – China, Hei Longjiang, Huma, Greater Khingan Range, III on *Q. mongolica*, 28 Jul 2000, J.Y. Zhuang, HMAS242639 (holotype).

GenBank accession numbers from holotype – SSU: OM745991; ITS: OM746423.

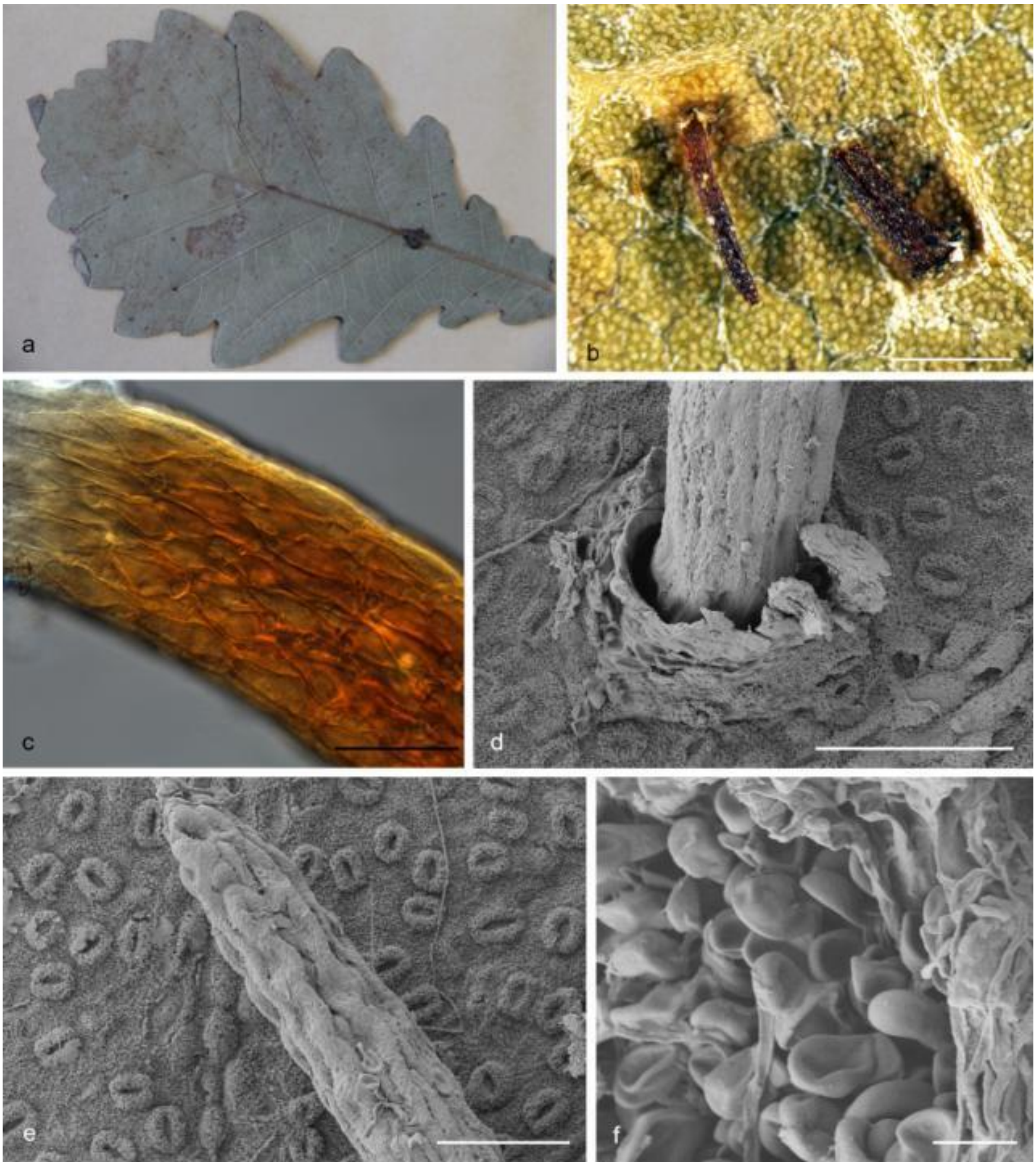

Figure 8 – Morphology of *Cronartium mongolicum*. a Hypophyllous telia on *Q. mongolica*. b Hair-like telia on leaf surface. c Section of a telium observed by LM. d, e Hair-like telia observed by SEM. f Capitate paraphyses in uredinium. Scale bars: b = 200 µm, c = 50 µm, d–e = 150 µm, f = 20 µm.

Additional material examined – China, Hei Longjiang, Huma, Greater Khingan Range, III on *Q. mongolica*, 28 Jul 2000, J.Y. Zhuang, HMAS82418 & HMAS82417; China, Hei Longjiang, Tahe, Greater Khingan Range, III on *Q. mongolica*, 2 Sept 2015, P. Zhao, ZP-R7.

Hosts range and geographical distribution confirmed in this study – *Q. mongolica* – China.

Notes – In the phylogenetic analysis *Cronartium mongolicum* was sister to *C. myricae* and *C. orientale* (Fig. 1C). Morphologically, it differs from *C. myricae* in the ornamentation of urediniospores and the dimension of teliospores (38–71 × 13–22 µm vs 32–55 × 10–17 µm); from *C. orientale* in the dimension of urediniospores (16–25 × 12–19 µm vs 22–34 × 11–19 µm), the length of telia (4.0–21.5 mm vs 2–3.8 mm), the dimension of teliospores (38–71 × 13–22 µm vs 39–83 × 10–21 µm), and the number of teliospores in the cross-section of telia (6–9 vs 9–14). This species was found with its telial stage on *Q. mongolica* in China (Table 2).

Cronartium murrayanae P. Zhao, X. Qi, & L. Cai, sp. nov. Fig. 9

MycoBank number: MB842420; Facesoffungi number: FoF 12569

Etymology – Epithet refers to the host species on which the type specimen was collected.

Spermogonia not found. Aecia hypophyllous, light brown, 0.2–0.6 mm, becoming erumpent, peridial cells globose or ellipsoid, 18–26 × 13–17 µm, cell walls about 2–4 µm thick, outer walls smooth, inner walls verrucose, warts annulate, 2–3 annuli, aeciospores borne singly, ellipsoid, obovoid, or subglobose, 29–62 × 11–22 µm, wall hyaline, with apparent tips at apex, 2.0–3.0 µm thick including verrucae connected by filaments, densely verrucose, warts annulate, 1–2 annuli, with obviously smooth area on surface, contents yellow. Uredinia and telia not found.

Type – USA, Wyoming, III on *P. murrayana*, 24 Jul 1922, L.E. Wehmeyer, MICH301494 (holotype).

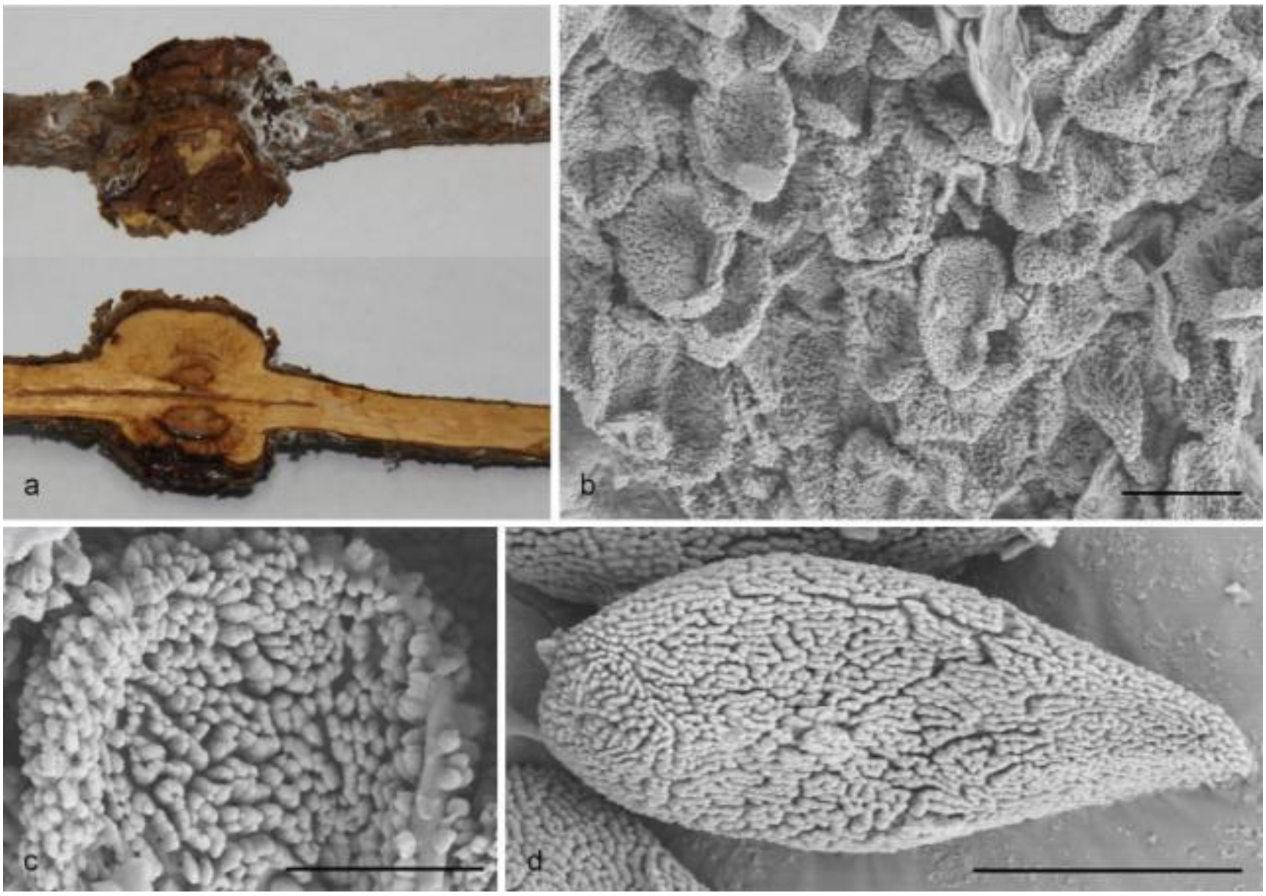

Figure 9 – Morphology of *Cronartium murrayanae*. a Aecia on *P. murrayana*. b Ellipsoid or globose peridial cells observed by SEM. c Ornamentation of peridial cells observed by SEM. d Ellipsoid or obovoid aeciospore observed by SEM. Scale bars: b = 20 µm, c = 5 µm, d = 20 µm.

GenBank accession numbers from holotype – SSU: OM745993; ITS: OM746425; LSU: OM746590; CO3: OM721416.

Additional material examined – Canada, Alberta, 0, I on *P. murrayana*, 5 Jul 1907, E.W.D. Holway, FLAS-F-4906; USA, Colorado, 0, I on *P. murrayana*, 15 Aug 1906, Bartholomew, FLAS-F-4907; USA, Wyoming, 0, I on *P. murrayana*, 24 Jul 1922, L.E. Wehmeyer, MICH301496.

Hosts range and geographical distribution confirmed in this study – *P. murrayana* – Canada, USA.

Notes – In the phylogenetic tree (Fig. 1B), *C. murrayanae* is phylogenetically close to *C. comandrae* and *C. pyriforme*. Morphologically, it differs from these two species in the dimension and shape of peridial cells, and a detailed morphological comparison was provided in the notes to *C. comandrae.* Previously, *C. coleosporioides*, *C. comptoniae* and *C. harknessii* have been reported on *P. murrayana* (Farr & Rossman 2021), but these species are phylogenetically distinct and morphologically distinguishable from *C. murrayanae*.

Cronartium myricae P. Zhao, X. Qi, & L. Cai, sp. nov. Fig. 10

MycoBank number: MB842421; Facesoffungi number: FoF 12570

Etymology – Epithet refers to the host species on which the type specimen was collected.

Spermogonia and aecia not found. Uredinia hypophyllous, 0.2–0.5 mm, not apparently forming columns on leaves, urediniospores ovoid or ellipsoid, 18–30 × 15–20 µm, wall echinulate, with apparent smooth regions, germ pores mostly scattered, inconspicuous, ostiolar cells apparent, erumpent on leaf surface, forced up to dome. Telia with hair-like columns, 0.7–1.0 mm long, straight or slight curved, bright yellow, teliospores oblong, 30–51 × 12–17 µm, catenulate, wall colorless, 0.5–1.3 µm thick, without surface ornamentation.

Type – China, Hubei, Shennongjia, III on *M. gale*, 9 Sept 1984, L. Guo, MICH253505 (holotype).

GenBank accession numbers from holotype – SSU: OM745996; ITS: OM746428; LSU: OM746593; CO3: OM721419.

Additional materials examined – Canada, British Columbia, II, III on *M. gale*, 20 Oct 1927, Partington, FLAS-F-24498; Canada, Ontario, II, III on *M. gale*, 6 Aug 1956, R.F. Cain, NYBG449422; Canada, Ontario, II, III on *M. gale*, 17 Sept 1957, R.F. Cain, NYBG449415; USA, Connecticut, II, III on *Myrica* sp., 15 Aug 1887, A.B. Seymour, FLAS-F-07017; USA, Michigan, II, III on *M. asplenifolia*, 12 Aug 1922, D.V. Baxter, MICH253485; USA, Maine, II, III on *M. gale*, 12 Oct 1900, P.L. Ricker, FLAS-F-07016; USA, New Hampshire, II, III on *M. asplenifolia*, 1 Sept 1891, W.G. Farlow, HMAS43576; USA, New Hampshire, II, III on *Myrica* sp., Sept 1891, W.G. Farlow, HKAS35062; USA, Wisconsin, III on *M. asplenifolia*, 31 Aug 1919, J.J. Davis, ISC351966 (ISC-F-0068287).

Hosts range and geographical distribution confirmed in this study – *M. asplenifolia* – USA; *M. gale* – Canada, USA.

Notes – In the phylogenetic tree (Fig. 1C), *C. myricae* formed an independent clade close to *C. mongolicum* and *C. orientale*. Morphologically, it differs from two species in the ornamentation and dimension of urediniospores and teliospores (Fig. 10). Previously, *C. flaccidum* (syn. *C. asclepiadeum*) was reported on *Myricales* species (Peterson 1973), but *C. myricae* was phylogenetically distinct from *C. flaccidum* (Fig. 1C-D). Moreover, it is morphologically distinct in its uredinia with apparent ostiolar cells and urediniospores with smooth regions (Fig. 10).

The rust fungus on three *Myrica* species (i.e., *M. asplenifolia*, *M. californica* and *M. gale*) was previously recognized as *C. comptoniae*, however, our research revealed that *C. myricae* on *Myrica* species was phylogenetically distinct from *C. comptoniae* (Fig. 1B). Morphologically, *C. myricae* differs from *C. comptoniae* in its uredinial morphology.

Cronartium occidentale Hedgc., Bethel & N.R. Hunt, J. Agric. Res., Washington 14: 415. 1918. Fig. 11

MycoBank number: MB247898

Synonym – *Peridermium occidentale* Hedgc., Bethel & N.R. Hunt, J. Agric. Res., Washington 14: 415. 1918.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, peridia 0.5–1.5 µm long, peridial cells rhomboid, 26–45 × 14–26 µm, outer walls smooth, wall 1.5–5.5 µm thick, inner walls small papillaes and side walls moderately rugose, verrucose, aeciospores globose, broadly ellipsoid, 17–34 × 13–24 µm, wall 2.5–4.0 µm, wall coarsely verrucose, warts annulate, 3–5 annuli, variable in shape, cylindrical, or joined to form ridges or appearing labyrinthine, with small bumps on top. Uredinia hypophyllous, urediniospores obovate, broadly ellipsoid, 22–34 × 11–19 µm, wall 1.0–3.0 µm thick, echinulate, germ pores mostly scattered, inconspicuous. Telia with cornute columns, 0.4–1.2 mm long, straight, bright yellow, cross-section of telia with 9–14 teliospores, teliospores oblong, 39–83 × 10–21 µm, catenulate, wall brownish, with smooth surface, 0.6–4.5 µm thick. Basidia external.

Figure 10 – Morphology of *Cronartium myricae*. a Hypophyllous uredinia and telia on *Myrica gale*. b Uredinia with apparent ostiolar cells. c Urediniospores with smooth regions. d hair-like telia observed by SEM. Scale bars: b = 200 µm, c = 20 µm, d = 200 µm.

Type – USA, Colorado, III on *R. aureum*, 15 Sept 1917, E. Bethel, BPI 034673 (holotype).

Epitypification – USA, Wyoming, III on *R. aureum*, 1 Oct 1955, W.G. Solheim, MICH253481 (epitype designated here, MBT10004992).

GenBank accession numbers from epitype – SSU: OM745999; ITS: OM746431; LSU: OM746596; CO3: OM721422.

Additional material examined – USA, California, III on *R. grandfolii*, 19 Jun 1920, E. Bethel, MICH253479; USA, California, III on *R. velutinum*, 4 Aug 1922, E. Bethel, FLAS-F-45172; USA, Colorado, III on *R. odoratum*, 28 Sept 1923, E. Bethel, MICH253477; USA, Colorado, III on *R. odoratum*, 7 Aug 1923, L. Bonar, HKAS35470.

Hosts and geographical distribution confirmed in this study – *P. edulis* – USA; *P. monophylla* – USA; *R. aureum* – USA; *R. cereum* – USA; *R. gandfalii* – USA; *R. odoratum* – USA; *R. velmtiunm* – USA.

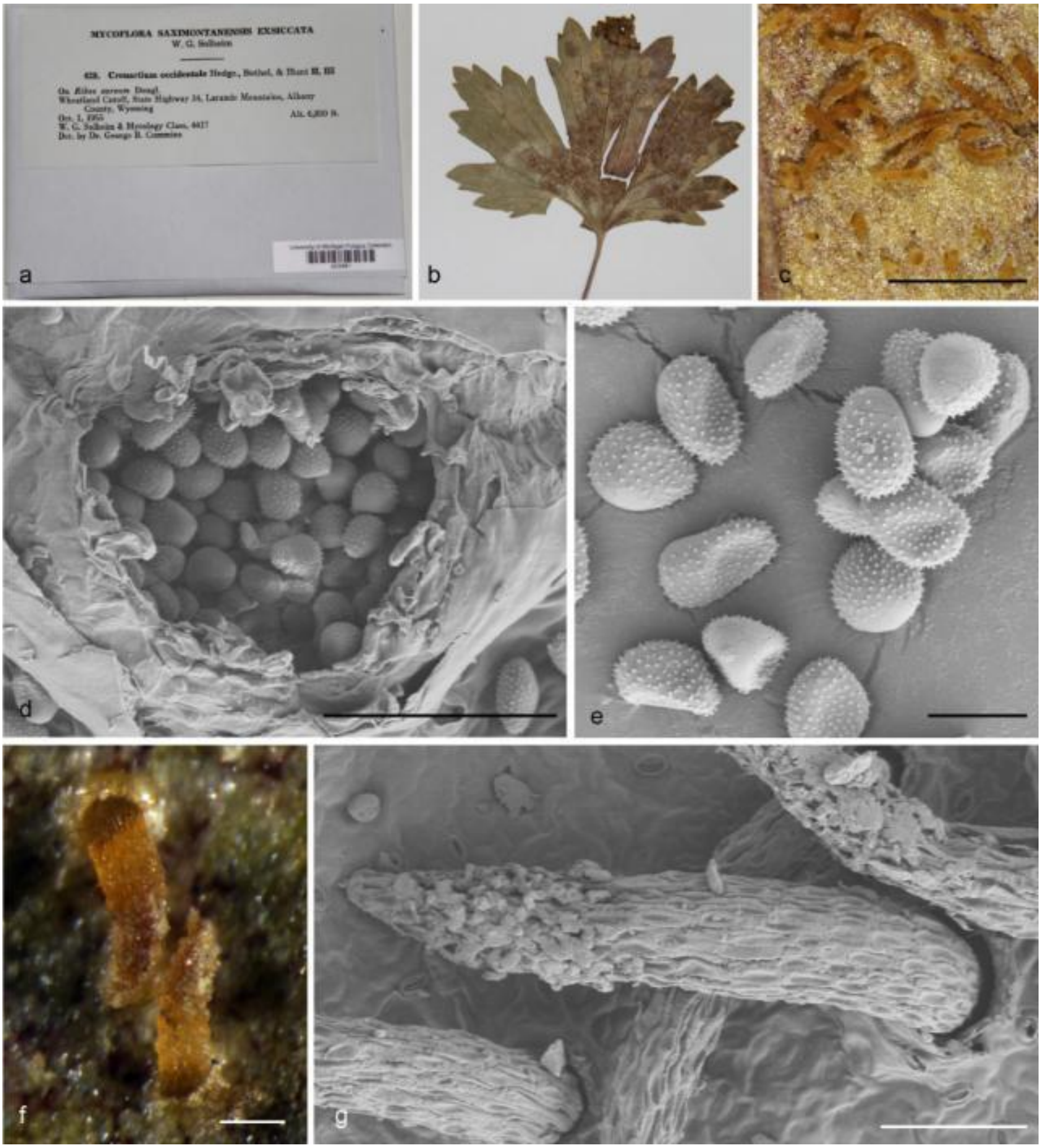

Figure 11 – Morphology of *Cronartium occidentale*. a Label of epitype specimen. b Hypophyllous telia on *R. aureum*. c Uredinia and hair-like telia observed on *R. aureum*. d Uredinium observed by SEM. e Obovate or broadly ellipsoid urediniospores with smooth regions. f Hair-like telia. g Telia observed by SEM. Scale bars: c = 1.00 mm, d = 100 µm, e = 20 µm, f–g = 200 µm.

Notes – In the phylogenetic tree (Fig. 1B), *C. occidentale* is closer to several timber rusts, including *C. appalachianum*, *C. arizonicum* and *C. comptoniae*. Morphologically, it differs from these species in the shape of aecia, dimension of peridial cells (26–45 × 14–26 µm vs 19–66 × 14–28 µm, 22–85 × 18–33 µm, 49–83 × 16–29 µm) and dimension of teliospores (39–83 × 10–21 µm vs 28–36 × 10–15 µm, 30–70 × 9–19 µm, 32–55 × 10–17 µm). We confirmed the host alternation of *C. occidentale* between two *Pinus* species and five *Ribes* species in North America (Table 2). Due to the potential threats to pine forests, more attention needs to be paid to the inspection of this pathogen in Asian and European countries.

Cronartium orientale S. Kaneko, Mycoscience 41(2): 116. 2000.

MycoBank number: MB464621

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, on globose or sub-globose galls on trunks or branches, large, irregular shape, yellow, peridial cells ellipsoid or rhomboid, 42–71 × 16–32 µm, walls 3.0–5.5 µm thick, verrucose, with irregular warts, aeciospores ellipsoid, obovoid, or subglobose, 18–25 × 13–22 µm, walls 1.3–2.0 µm thick, densely verrucose, occasionally with a smooth spot, warts annulate, 6–7 annuli, cylindrical, joined to form ridges or appearing labyrinthine, with small bumps on top. Uredinia hypophyllous, scattered, 0.2–0.4 mm, yellow, covered by inconspicuous hemispherical peridia, urediniospores obovoid or ellipsoid, 16–34 × 14–21 µm, wall hyaline, 1.0–2.0 µm thick, echinulate, germ pores scattered, 4–7. Telia hypophyllous, scattered, forming filiform columns, straight or slightly curved, 2.0–3.8 mm, cross-section of telia with 3–7 teliospores, brown, teliospores oblong or ellipsoid, 31–59 × 13–22 µm, wall brown, smooth, 2.5–4.5 µm. Basidia external.

Type – Japan, Tottori, Yokotemichi, III on *Q. crispula*, 19 Oct 1973, S. Kaneko, TSH-R1709 (Isotype).

Additional material examined – China, Anhui, Chuxian, 0, I on *P. hwangshanensis*, Aug 1992, Y.R. Lin, HMAS79083; China, Gansu, Tianshui, III on *Q. liaotungensis*, 12 Sept 1992, J.Y. Zhuang, HMAS77666; China, Hainan, III on *Q. variabilis*, 10 Dec 2009, J.Y. Zhuang, HMAS242500; China, Heilongjiang, III on *Q. mongolica*, 28 Jul 2000, J.Y. Zhuang, HMAS82417; China, Jiangsu, III on *Quercus* sp., 5 Jun 1928, F.L. Tai, HMAS14269; China, Jiangsu, III on *Q. variabilis*, 10, Jun 1932, S.C. Teng, HMAS6746; China, Jiangxi, III on *Q. glandulifera* var. *brevipetiolata*, 20 Oct 1996, S.X. Wei, HMAS82717; China, Shaanxi, III on *Q. variabilis*, 23 Sept 1991, J.Y. Zhuang & S.X. Wei, HMAS74350; China, Sichuan, III on *Quercus* sp., 1 Oct 1958, Y.S. Xing, HMAS55119; China, Sichuan, III on *Quercus* sp., 9 Sept 1958, Y.N. Yu, HMAS34939; China, Sichuan, III on *Quercus* sp., 30 Sept 1989, J.Y. Zhuang, HMAS64220; China, Tibet, Bomi, 0, I on *P. densata*, 20 Jul 1983, J.Y. Zhuang, HMAS45784; China, Tibet, Bomi, III on *Q. aquifolioides*, 27 Jul 2010, J.Y. Zhuang, HMAS242640, HMAS242641 & HMAS242642; China, Yunnan, III on *Q. spinosa*, 1 Nov 1958, S.J. Han, HMAS34937; China, Yunnan, III on *Q. variabilis*, 7 Apr 1986, M. Zang, HKAS 17705; Yunnan, III on *Q. variabilis*, 2 Aug 1995, G. Durrieu, HKAS29569; China, Yunnan, III on *Q. spinosa*, 31 Jul 1995, G. Durrieu, HKAS29386.

GenBank accession numbers – SSU: OM746008; ITS: OM746438; LSU: OM746604; CO3: OM721432 (HMAS242500).

Hosts and geographical distribution confirmed in this study – *P. hwangshanensis* – China; *P. densata* – China; *Q. aquifolioides* – China; *Q. crispula* – Japan; *Q. glandulifera* – China; *Q. liaotungensis* – China; *Q. spinosa* – China; *Q. semicaipifolia* – China; *Q. variabilis* – China.

Additional hosts and geographical distribution reported in previous studies – *Castanea crenata* – Japan; *P. densiflora* – China, Japan, Russia; *P. thunbergii* – Japan; *Q. acutissima* – China; *Q. aliena* – China; *Q. fabri* – China; *Q. glauca* – Japan; *Q. phellos* – Japan; *Q. rubra* – Japan; *Q. serrata* – Japan; *Q. sponosa* – China; *Q. variabilis* – Japan (Kaneko 2000).

Notes – Pine-oak rust in China and Japan has long been identified as *C. quercuum*, despite discrepancies in morphology, pathogenicity, and molecular data between Asian and American specimens (Kaneko 1991, Nakamura et al. 1998). Kaneko (2000) separated the Asian pine-oak rust as a distinct species, *C. orientale*. Here we confirmed the phylogenetic distinction between the two species (Fig. 1B, C). Morphologically, *C. orientale* differs from *C. quercuum* in the dimension of peridial cells (32–57 × 12–22 µm vs 42–71 × 16–32 µm) and aeciospores (23–33 × 16–23 µm vs 18–25 × 13–22 µm). The two species have different host alternation and geographic distribution (Table 2).

Figure 12 – Morphology of *Cronartium peridiatum*. a Label of holotype specimen. b Peridermioid aecia on *P. strobus*. c Ellipsoid, obovoid, or subglobose aeciospore observed by SEM. d Nailhead-like verrucae on aeciospore. e Ellipsoid or oblong peridial cells observed by SEM. f Rugose surface of peridial cells inner wall. g Uredinia and telia on *R. nigrum*. h Hair-like telia. i Telia observed by SEM. j Urediniospore observed by SEM. k Section of a telium observed by LM. l Telium with ostiolar cells observed by SEM. Scale bars: c = 10 µm, d–f = 20 µm, i = 200 µm, j = 5 µm, k–l = 50 µm.

Cronartium peridiatum P. Zhao & L. Cai, sp. nov. Fig. 12

MycoBank number: MB842422; Facesoffungi number: FoF 12571

Etymology – Epithet refers to species having special perdial cells compared to *C. ribicola*.

Spermogonia not found. Aecia peridermioid, intracortical in origin, erumpent, peridia cylindric, 5–12 mm high, peridial cells ellipsoid or oblong, 28–49 × 14–21 µm, outer layers smooth, inner wall rugose, aeciospores borne singly, ellipsoid, obovoid, or subglobose, 14–25 × 11–19 µm, wall 2.0–3.0 µm thick including verrucae connected by filaments, verrucae 1.4–2.5 µm high, densely verrucose, nailhead-like verrucae with 2–4 annuli, with obviously smooth area on surface. Uredinia usually lacked. Telia hypophyllous, hair-like columns, 0.3–1.5 mm long, straight or slight curved, light yellow, cross-section of telia with 7–12 teliospores, teliospores 30–80 × 8–20 µm, oblong, catenulate, wall brown, 0.3–1.6 µm thick, without surface ornamentation.

Type – Canada, Ontario, 0, I on *P. strobus*, May 1952, collector unknown, NYBG267053 (holotype).

GenBank accession numbers from holotype – SSU: OM746014; ITS: MK208298; LSU: MK193829; CO3: OM721437.

Additional material examined – Bolivia, III on *Eupatorium subscandens*, 25 May 1920, E.W.D. Holway, MICH278063; Bolivia, III on *Eupatorium odoratum*, 23 Dec 1927, H. Sydow, MICH278062; Canada, Alberta, III on *Ribes* sp., 16 Sept 1998, H. Schalkwijk, HMAS86824; Canada, Quebec, III on *R. nigrum*, F. Godbout, NYBG267052; Canada, Quebec, III on *Ribes* sp., Aug 1950, S.M. Pady, NYBG267061; China, Heilongjiang, III on *R. mandschuricum*, 28 Aug 1977, L.P. Shao, HMAS38589; China, Xinjiang, III on *Ribes* sp., date unknown, Z.K. Liu, HMAS37742; USA, New York, III on *R. nigrum*, 18 Aug 1932, W.L.C. Muenscher, NYBG267051; USA, New York, III on *Ribes* sp., 31 Jul 1951, S.M. Pady, NYBG267057.

Hosts and geographical distribution confirmed in this study – *Eupatorium odoratum* – Bolivia; *Eupatorium subscandens* – Bolivia; *R. mandschuricum* – China; *R. nigrum* – Canada; *Ribes* sp. – China.

Notes – In the phylogenetic tree (Fig. 1A), *C. peridiatum* was allied to *C. ribicola*. Morphologically, it differs from *C. ribicola* in the dimension of aeciospores (14–25 × 11–19 µm vs 22–38 × 16–27 µm). In addition, peridial cells in *C. peridiatum* have rugose inner wall, whereas those in *C. ribicola* have 3–5 annuli. Aecial stage of *C. peridiatum* is found on *P. strobus*, while telial stage is found on *Eupatorium odoratum*, *R. nigrum*, *R. mandschuricum* and *Pedicularis* sp. (Table 2). Previously, *C. sahoanum*, *C. yamabense*, and *C. ribicola* were reported on *P. strobus*, but they differ from *C. peridiatum* in the morphology of teliospores, shape of verrucae on aeciospores and peridial cells (Hiratsuka et al. 1992). *Cronartium andinum*, *C. eupatorinum*, and *C. praelongum*, have been found on *Eupatorium odoratum* (Sydow & Sydow 1915), but *C. peridiatum* differs from these species in the dimension of teliospores (30–80 × 8–20 µm vs 70–100 × 11–14 µm, 28–44 × 13–20 µm, 12–15 × 8–10 µm).

Cronartium pini (Willd.) Jørst., Norsk. Acad. Oslo Math. Nat. Kl. 10: 106. 1925.

MycoBank number: MB416318

Synonyms – *Aecidium pini* (Willd.) Pers., Syn. Meth. Fung. (Göttingen) 1: 213. 1801.

Endocronartium pini (Willd.) Y. Hirats., Can. J. Bot. 47(9): 1494. 1969.

Peridermium pini (Willd.) J.C. Schmidt & Kunze, Deutschl. Schwämme, Sechste Lieferung: 4. 1817.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, spread over a rather larger area of the shoot, 2.5–6.0 mm long, on trunks or branches, peridia 2.0–3.5 mm high, peridial cells isodiametric, 15–41 × 13–21 µm, walls about 3.5–6.0 µm thick, verrucose, aeciospores ellipsoid or polyhedral, 24–33 × 15–24 µm, walls 3.5–5.0 µm thick, most of their surface verrucose. Uredinia not found. Telia hypophyllous, scattered, forming filiform columns, straight or slightly curved, 2.5–6.5 mm long, brown, teliospores oblong or ellipsoid, 23–45 × 8–15 µm, wall yellowish-brown, smooth, 0.4–1.2 µm thick. Basidia external.

Material examined – USA, Massachusetts, 0, I on *P. rigida*, 20 Aug 1923, Cummins & Seymour, FLAS-F-5306.

GenBank accession numbers – ITS: KU320169, AY566270, KJ959593, KJ959594.

Hosts and geographical distribution confirmed in this study – *Bartsia alpina* – Finland; *Melampyrum nemorosum* – Finland; *P. rigida* – USA; *P. sylvestris* – Finland, Greece, Italy.

Notes – To date, five *Cronartium* species (*C. asclepiadeum*, *C. flaccidum*, *C. pini*, *C. quercuum* and *C. ribicola*) have been described from *P. sylvestris* in Europe (Farr & Rossman 2021). Our results are consistent with Wijesinghe et al. (2019), who recognized European *Cronartium* on *Bartsia alpina* and *Melampyrum nemorosum* as *C. pini*.

Figure 13 – Morphology of *Cronartium pyriforme*. a Label of epitype specimen. b Aecia caulicolous and erumpent from the bark of *P. contorta*. c Oblong-pyriform aeciospores observed by SEM. d Ornamentation of aeciospore observed by SEM. e Rugose surface of peridial cells inner wall. f Hair-like telia on the leaf and stem of *Com. pallida*. g Hair-like telia. h Telia with ostiolar cells observed by SEM. Scale bars: c = 20 µm, d = 2 µm, e = 10 µm, g = 1 mm, h = 100 mm.

Cronartium pyriforme (Peck) Hedgc. & Long, privately printed at Washington D.C., 3. 1914.

Fig. 13

MycoBank number: MB416319

Basionym – *Peridermium pyriforme* Peck [as ‘piriforme’], Bull. Torrey Bot. Club 6(2): 13. 1875.

Spermogonia not found. Aecia caulicolous, erumpent from the bark, on trunks or branches, peridia tubular, peridial cells ellipsoid, globose or isodiametric, 34–57 × 16–28 µm, wall 2.5–3.5 µm thick, verrucose, aeciospores oblong-pyriform, broadly ellipsoid, fusiform, with apparent tips at apex, 43–69 × 14–26 µm, wall verrucose, 0.5–2.5 µm thick, warts with 1 annulus, variable in shape, some with a central spine. Uredinia usually lacked. Telia amphigenous or caulicolous, yellowish or brown, columnar, 0.5–1.2 mm, teliospores ellipsoid or elongate, 29–44 × 11–17 µm, catenulate, wall 0.5–1.5 µm thick. Uredinia and telia not found.

Type – USA, New Jersey, III on *P. contorta*, 7 Sept 1884, J.B. Ellis, NYS-F-002537, (syntype).

Epitypification – USA, Wyoming, III on *P. contorta*, 15 Aug 1887, A. Jacobsen, MICH253420 (epitype designated here, MBT10004993).

GenBank accession numbers from epitype – SSU: OM746023; ITS: OM746451; LSU: OM746617; CO3: OM721446.

Additional material examined – Canada, III on *Comandea umbellata*, 11 Sept 1977, D. Munro, HMAS38375; USA, Montana, III on *Com. pallida*, Aug 1912, J.E. Kirkwood, FLAS-F-24500; USA, Wyoming, III on *Com. pallida*, 23 Aug 1949, W.G. Solheim, MICH253360; USA, Wyoming, III on *Comandea umbellata*, 20 Aug 1923, B.B. Kanouse, FLAS-F-22688.

Hosts and geographical distribution confirmed in this study – *Com. pallida* – USA; *Com. umbellata* – Canada, USA; *P. contorta* – USA.


74356
中国科学院微生物所真菌标本室
标本号 74356
学名 Cronartium quercuum (Berk.) Miyabe ex Shirai
寄主 Quercus aliena Bl.
采集地 Shaanxi: Fuping(佛平)
采集日期 1991 IX 26
采集人 Zhuang Jian-yun & Wei Shu-xia
采集号 4538
定名人 Zhuang Jian-yun

Figure 14 – Morphology of *Cronartium qinlingense*. a. Label of holotype specimen. b Hypophyllous telia on *Q. aliena*. c Hair-like telia. d Section of a telium observed by LM. e Telia observed by SEM. Scale bars: c = 500 µm, d = 20 µm, e = 100 µm.

Notes – Peck (1875) described *Per. pyriforme* on *P. virginiana*, and thereafter, Hedgcock & Long (1913, 1915) confirmed that *Per. pyriforme* was the aecial stage of *Cronartium* by checking the type material and inoculation experiments. As a result, a new combination, *C. pyriforme*, was introduced. *Cronartium pyriforme* has long been considered as a synonym of *C. comandrae* due to similar morphology and same host range (Peterson 1967). In our phylogenetic tree (Fig. 1B), *C. pyriforme* formed a separate clade sibling to *C. comandrae* and *C. murrayanae*. Morphologically, it differs from *C. comandrae* in the dimension of uredinio spores and teliospores (Fig. 13).

Cronartium qinlingense P. Zhao & L. Cai, sp. nov. Fig. 14

MycoBank number: MB842423; Facesoffungi number: FoF 12572

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

Spermogonia, aecia and uredinia not found. Telia hypophyllous, in a filamentous column, 0.40–2.5 mm long, brown, straight, or ellipsoid, curved, cross-section of telia with 3–5 teliospores, teliospores elongated or fusiform, 18–44 × 8–23 µm, walls almost hyaline, smooth, 0.3–2.0 µm.

Type – China, Shaanxi, Foping, Qinling Mountains, III on *Q. aliena*, 26 Sept 1991, J.Y. Zhuang & S.X. Wei, HMAS74356 (holotype).

GenBank accession numbers from holotype – SSU: OM746026; ITS: OM746454; LSU: OM746620; CO3: OM721449.

Additional material examined – China, Shaanxi, Foping, Qinling Mountains, III on *Q. aliena*, 1 Aug 1976, J.Y. Zhuang & S.X. Wei, HMAS4538; China, Shaanxi, Ningshan, Qinling Mountains, III on *Q. aliena*, 1 Aug 1976, T.Y. Zhang, HMAS56423; China, Shaanxi, Ningshan, Qinling Mountains, III on *Q. aliena var. acuteserrata*, 1 Aug 1976, T.Y. Zhang, HMAS20356.

Hosts and geographical distribution confirmed in this study – *Q. aliena* – China.

Notes – *Cronartium qinlingense* is phylogenetically close to *C. flaccidum* and *C. fusiforme* (Fig. 1D). Morphologically, it can be distinguished from *C. flaccidum* and *C. fusiforme* by the number of teliospores in a cross-section of the telia and the dimension of teliospores. Previously, *C. quercuum* and *C. orientale* were reported on *Q. aliena*, but *C. qinlingense* differs from *C. quercuum* in the number of teliospores in cross-section of telia (3–5 vs 7–10), and from *C. orientale* in the dimension of teliospores (18–44 × 8–23 µm vs 31–59 × 13–22 µm), color and wall thickness of teliospores.

Cronartium quercuum (Berk.) Miyabe ex Shirai, Bot. Mag., Tokyo 13: 74. 1899.

MycoBank number: MB240633

Synonyms – *Cronartium quercuum* f.sp. *banksianae* Burds. & G.A. Snow, Mycologia 69(3): 505. 1977.

Cronartium quercus (Brond.) J. Schröt. ex Arthur, N. Amer. Fl. (New York) 7(2): 122. 1907.

Endocronartium harknessii (J.P. Moore) Y. Hirats., Can. J. Bot. 47(9): 1493. 1969.

Peridermium harknessii J.P. Moore [as ‘harknessi’], in Harkness, Bull. Calif. Acad. Sci. 1 (no. 1): 37. 1884.

Spermogonia not found. Aecia gall shape or irregularly shaped, on trunks or branches, 3–10 mm long, containing powdery yellow-orange spores, peridial cells ovoid, ellipsoid, or oblong, 32–57 × 12–22 µm, consisting of two layers, outside surface of peridia smooth, inside verrucose, walls 1.0–3.5 µm thick, evenly thickened, aeciospores obovoid or ellipsoid, 23–33 × 16–23 µm, wall 1.5–3.5 µm thick, coarsely verrucose. Uredinia sometimes lacked, hypophyllous, scattered or aggregated, yellow, covered by hemispherical peridial cells, urediniospores obovoid or ellipsoid, 16–30 × 14–21 µm, wall hyaline, 2.0–3.5 µm thick, echinulate, germ pores scattered. Telia hypophyllous, in a filamentous column, 0.40 mm long, brown, straight, or curved, cross-section of telia with 7–10 teliospores, teliospores elongated or fusiform, 20–47 × 7–23 µm, walls hyaline, with smooth surface, 0.3–2.0 µm.

Type – USA, Pennsylvania, III on *Q. tinctoriae*, date unknown, E. Michener, NYBG69678 (lectotype).

Additional material examined – Canada, Ontario, III on *Q. rubra*, 12 Aug 1929, H.S. Jackson, MICH253530; Honduras, III on *Quercus* sp., 27 Jul 1936, E.B. Mains, MICH253529; USA, Arizona, III on *Q. hypoleuca*, 26 May 1922, E. Bethel, FLAS-F-45217; USA, Arkansas, III on *Q. alba*, 25 Sept 1908, Bartholomew, FLAS-F-07038; USA, California, 0, I on *P. halepensis*,16 Mar 1942, K.H. Beach, MICH301230; USA, California, III on *Q. agrifolia*, 1 Mar 1903, C.F. Baker, FLAS-F-07042; USA, Delaware, III on *Q. marylandica*, 9 Jul 1907, H.S. Jackson, NYBG449410; USA, Delaware, III on *Q. digitata*, 9 Jul 1907, H.S. Jackson, FLAS-F-07036; USA, Florida, 0, I on *P. taeda*, 15 Feb 1935, G.F. Weber, FLAS-F-17047; USA, Florida, 0, I on *P. taeda*, 21 Feb 1927, Weber & West, FLAS-F-07233; USA, Florida, 0, I on *P. clausa*, 27 Feb 1938, A.S. Rhoads, FLAS-F-21922; USA, Florida, III on *Q. chapmanii*, 19 May 1935, G.F. Weber, FLAS-F-17042; USA, Florida, III on *Q. geminate*, 17 Apr 1938, G.F. Weber, FLAS-F-20414; USA, Florida, III on *Q. laurifolia*, 17 Apr 1938, G.F. Weber, FLAS-F-20411; USA, Florida, III on *Q. nigra*, 17 Apr 1927, Weber & West, FLAS-F-07044; USA, Florida, III on *Q. virginiana*, 19 Apr 1935, G.F. Weber, FLAS-F-17048; USA, Kansas, III on *Q. macrocarpa*, 15 Oct 1951, C.T. Rogerson, NYBG267644; USA, Kansas, III on *Q. macrocarpa*, 4 Jul 1908, A.O. Garrett, NYBG3106209; USA, Kansas, III on *Q. macrocarpa*, 31 Aug 1908, Bartholomew, FLAS-F-07039; USA, Kansas, III on *Quercus* sp., 31 Aug 1908, E. Bartholomew, NYBG3106210; USA, Maryland, 0, I on *P. virginiana* Mill, 5 Apr 1938, W.M. Epps, NYBG267642; USA, North Carolina, III on *Q. coccinea*, 28 Jun 1938, G.G. Hedgcock, FLAS-F-45200; USA, North Carolina, III on *Q. falcata*, 9 Jul 1909, B.B. Higgins, FLAS-F-07037; USA, Tennessee, III on *Q. imbricaria*, 7 Jul 1937, H.M. Jennison, ISC395258 (ISC-F-0068304); USA, Tennessee, III on *Q. velutina*, 24 Jun 1974, L.R. Heeler, FLAS-F-17046; USA, Texas, III on *Quercus* sp., 15 Apr 1934, Tracy, HKAS35628; USA, Washington, III on *Q. borealis*, 23 Jun 1923, G.G. Hedgcock, FLAS-F-45180; USA, Washington, III on *Q. borealis*, 16 May 1929, G.G. Hedgcock, FLAS-F-45188; USA, Tennessee, III on *Q. borealis var. maxima*, 24 Jun 1934, L.R. Heeler, FLAS-F-17044; USA, Washington, III on *Q. macrocarpa*, 17 May 1929, G.G. Hedgcock, FLAS-F-45232; USA, West Virginia, III on *Q. coccinea*, 1 Jul 1910, R. & E. Cook, FLAS-F-07033; West USA, Virginia, III on *Q. velutina*, 1 Jul 1910, R. & E. Cook, FLAS-F-07034; USA, Virginia, III on *Q. coccinea*, 20 Jun 1919, G.G. Hedgcock, MICH253337; USA, Virginia, III on *Q. coccinea*, 1 Jul 1910, R. Cook, MICH253547.

GenBank accession numbers – SSU: OM746034; ITS: OM746462; LSU: OM746628; CO3: OM721457 (MICH301230).

Hosts and geographical distribution confirmed in this study – *P. banksiana* – USA; *P. clausa* – USA; *P. contorta* – USA; *P. halepensis* – USA; *P. leiophylla* – USA; *P. sylvestris* – Canada, USA; *P. taeda* – Canada, USA; *Q. alba* – USA; *Q. agrifolia* – USA; *Q. borealis* – USA; *Q. borealis var. maxima* – USA; *Q. chapmanii* – USA; *Q. coccinea* – USA; *Q. digitata* – USA; *Q. falcata* – USA; *Q. glandulifera* – Honduras; *Q. hypoleuca* – USA; *Q. marylandica* – USA; *Q. rubra* – Canada; *Quercus* sp. – Honduras; *Q. velutina* – USA.

Notes – *Cronartium quercuum* was first discovered on *Q. nigra* from the USA (Shirai 1899). Several North American species, *C. fusiforme*, *C. cerebrum*, *C. strobilinum*, and *C. conigenum*, were once treated as synonyms of *C. quercuum* due to their morphological similarities (Arthur 1934). With the exception of the invalid name *C. cerebrum*, several taxonomists considered other species as distinct (Cummins 1962, Peterson 1973). Herein, we confirmed that *C. quercuum* is phylogenetically distinct from *C. fusiforme*, *C. orientale* and *C. strobilinum*, and these species shows clear morphological differences in aecial morphology. In the phylogenetic tree (Fig. 1C), *C. quercuum* formed a distinct clade and included its endo-type relatives, which were once identified as *Endocronartium harknessii* (Hiratsuka 1969). Although Aime et al. (2018b) assigned this species to *Cronartium* (as *C. harknessii*), here we confirm it as a synonym of *C. quercuum*, which agrees with Vogler & Bruns (1998) and Wijesinghe et al. (2019).

Cronartium ribicola J.C. Fisch., Hedwigia 11: 182. 1872.

MycoBank number: MB452103

Spermogonia not found. Aecia caulicolous, on somewhat thickened areas of trunks or branches, 2–7 cm long, 2–3 cm wide, 2.0–2.5 cm high, peridial cell ellipsoid or linear-rhomboid, outer walls smooth or with small protuberances, inner wall warts annulate, 3–5 annuli, 26–32 × 16–22 µm, aeciospores ovoid to ellipsoid, 22–38 × 16–27 µm, walls warts annulate, 3–5 annuli, 2–3.5

µm thick. Uredinia hypophyllous, covered by hemispherical peridia, urediniospores ellipsoid, 19–35 × 14–23 µm, walls, echinulate, 2–3 µm thick, germ pores mostly bizonate, inconspicuous. Telia hypophyllous, usually arising from the center of uredinia, cylindrical, mostly curved, up to 2 mm long, 120–150 µm wide, orange-yellow, brown, teliospores oblong or cylindrical, cross-section of telia with 6–14 teliospores, 30–76 × 10–20 µm, walls hyaline, smooth, 2–3 µm thick. Basidia external, basidiospores echinulate.

Material examined – Canada, British Columbia, 0, I on *P. monticola*, 27 May 1959, M.Bell, UBC-F5879; Canada, British Columbia, III on *R. nigrum*, 17 Aug 1948, W. Jones, UBC-F5890; Canada, British Columbia, on *Ribes* sp., date unknown, B. Lawson, UBC-F5899; Canada, Ontario, III on *R. odoratum*, 29 Oct 1932, L.M. Hunter, NYBG267058; Canada, Ontario, III on *Ribes* sp., 1 Aug 1938, S.M. Pady, NYBG267056; Canada, Ontario, III on *Ribes* sp., Aug 1946, S.M. Pady, NYBG267059; Canada, Ontario, III on *R. nigrum*, 18 Aug 1924, H.N. Racicot, HMAS38376; Canada, South of Nose Lake, near Elmworth, Alta, 0, I on *P. coronata*, 12 Jul 1969, collector unknown, TSH-1094; China, Xinjiang, III on *R. nigrum*, 17 Aug 1986, J.Y. Zhuang, HMAS52870; China, Xinjiang, Altay Prefecture, III on *R. nigrum*, 26 Aug 2016, P. Zhao, ibid. ZP-R4, ZP-R332, ZP-R347, ZP-R352, ZP-R363, ZP-R453, ZP-R460, ZP-R464, ZP-R486, ZP-R492, ZP-R512, ZP-R524, ZP-R594; Japan, Hokkaido, Sapporo-shi, Hitsujiga, III on *R. sativum*, 5 Sept 1972, collector unknown, TSH-R17009; Japan, Nagano, III on *Pedicularis yezoensis*, 8 Sept 1990, M. Imazu, HMAS66843; Germany, Bayern, 0, I on *P. strobus*, 1 Mar. 1990, B. Koth & D. Triebel, HMAS67777; USA, California, III on *R. lobbii*, 14 Aug 1948, J.P. Tracy, ISC395271 (ISC-F-0068313); USA, California, III On *R. roezl* var. *cruentum*, 26 Aug 1949, J.P. Tracy, FLAS-F-44462; USA, California, III on *Ribes* sp., 15 Aug 1948, J.P. Tracy, FLAS-F-44435; Columbia, III on *R. nigrum*, 1 Jul 1918, R.H. Colley, NYBG449413; USA, California, III on *R. bracteosum*, 5 Sept 1948, J.P. Tracy, FLAS-F-43357; USA, California, III on *R. lobbii*, 26 Aug 1949, J.P. Tracy, FLAS-F-44460; USA, Connecticut, III on *R. nigrum*, 5 Oct 1916, G.P. Clinton, FLAS-F-23559; USA, Iowa, III on *R. missouriense*, 25 May 2000, L.H. Tiffany, ISC428956 (ISC-F-0079967); USA, Iowa, III on *Ribes* sp., 25 Jun 1976, L.H. Tiffany, ISC343765 (ISC-F-0079968); USA, Maine, III on *R. glandulosum*, 30 Aug 1929, H.J. Wilson, FLAS-F-17051; USA, New Hampshire, 0, I on *P. strobus*, 6 May 1918, L.O. Overholts, FLAS-F-07047; USA, New York, III on *R. nigrum*, 24 Oct 1906, F.C. Stewart, NYBG3106213; USA, New York, III on *R. nigrum*, Nov 1912, P. Spaulding, ISC351969 (ISC-F-0068308); USA, Oregon, III on *R. bracteosum*, 24 Jul 1935, J.R. Stevenson, UBC-F5886; Oregon, III on *Ribes* sp., 30 Jul 1932, L.M. Goodding, NYBG3106211; USA, Oregon, III on *Ribes* sp., 19 Jul 1927, W.T. Lund, NYBG3106212; Iowa 0, I on *P. albicaulis*, data known, Childs & Peace, FLAS-F-24493.

GenBank accession numbers – SSU: OM746056; ITS: OM746484; LSU: OM746650; CO3: OM721479 (MICH253525).

Hosts and geographical distribution confirmed in this study – *P. albicaulis* – USA; *P. coronata* – Canada; *P. monticola* – Canada, USA; *P. strobus* – Germany, USA; *Pedicularis yezoensis* – Japan; *R. bracteosum* – USA; *R. glandulosum* – USA; *R. missouriense* – USA; *R. nigrum* – Canada, China, USA; *R. odoratum* – Canada, USA; *R. roezlii var. cruentum* – USA; *R. sativum* – Japan.

Notes – In the phylogenetic tree (Fig. 1A), *C. ribicola* formed a well-supported clade sister to *C. peridiatum* and *C. ribis-taedae*. Morphologically, it differs from *C. peridiatum* in the dimension of aeciospores, shape and ornamentation of peridial cells; from *C. ribis-taedae* in the dimension of teliospores (30–76 × 10–20 µm vs 40–58 × 8–15 µm) and color of teliospores. *Cronartium ribicola* was first discovered on *R. aureum* from Germany, and then spread throughout Europe, North America, and East Asia (Kuprevich & Tranzschel 1957, Wilson & Henderson 1966, Hiratsuka et al. 1992, Zhang et al. 2010, Farr & Rossman 2021). We have confirmed its aecial and telial host range (Table 2), and this species was found in the northeast and northwest regions of China.

Cronartium ribis-taedae P. Zhao & L. Cai, sp. nov. Fig. 15

MycoBank number: MB842424; Facesoffungi number: FoF 12573

Etymology – Epithet refers to the host species on which the type specimen was collected.

Spermogonia not found. Aecia light brown, hypophyllous, 0.2–0.6 mm, becoming erumpent, aeciospores borne singly, ellipsoid, obovoid, or subglobose, 16–33 × 12–21 µm, wall 2.0–3.0 µm thick, verrucae connected by filaments, verrucae 1.4–2.5 µm, densely verrucose, nailhead-like verrucae with 3–5 annuli, with obviously smooth area on surface. Uredinia usually lacked, urediniospores occasionally accompanying with telia, echinulate, sometimes with smooth surface at apex. Telia hypophyllous, hair-like columns, 0.4–1.5 µm long, straight or slight curved, light yellow, cross-section of telia with 4–10 teliospores, teliospores oblong, 40–58 × 8–15 µm, catenulate, wall yellowish brownish, 0.5–1.3 µm thick, without surface ornamentation.

Type – China, Florida, 0, I on *P. taeda*, 27 Feb 1919, G.G. Hedgcock, FLAS-F-16581 (holotype).

GenBank accession numbers from holotype – SSU: OM746014; ITS: MK208298; LSU: MK193829; CO3: OM721437.

Additional material examined – China, Xinjiang, III on *R. nigrum*, 5 Sept 2004, J.Y. Zhuang, HMAS172046; Xinjiang, III on *Ribes* sp., 16 Aug 1986, J.Y. Zhuang, HMAS52871; USA, Florida, 0, I on *P. taeda*, 29 Mar 1928, A.N. Tissot, FLAS-F-7199; Florida, 0, I on *P. taeda*, 29 Mar 1928, A.N. Tissot, FLAS-F-7200; Florida, 0, I on *P. caramels*, 6 Mar 1918, G.G. Hedgcock, FLAS-F-16562; North Carolina, 0, I on *P. echinata*, 30 Apr 1916, G.G. Hedgcock, FLAS-F-16567; South Carolina, III on *Ribes* sp., 19 Apr 1916, G.G. Hedgcock, FLAS-F-16578.

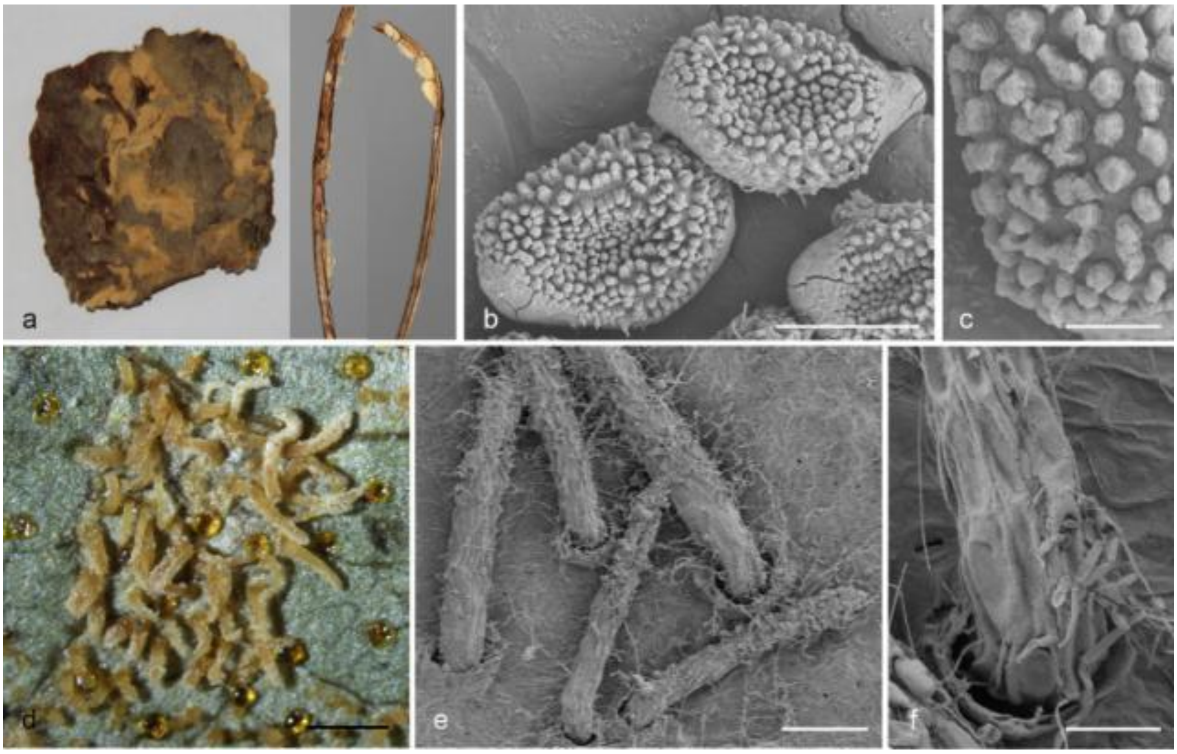

Figure 15 – Morphology of *Cronartium ribis-taedae*. a Aecia on stem and needle of *P. taeda*. b Ellipsoid, obovoid, or subglobose aeciospores observed by SEM. c Nailhead-like verrucae on aeciospores. d Hair-like telia. e Telia observed by SEM. f Teliospores with smooth surface. Scale bars: b = 10 µm, c = 2 µm, d = 500 µm, e = 100 µm, f = 50 µm.

Hosts and geographical distribution confirmed in this study – *P. caramels* – USA; *P. echinata* – USA; *P. taeda* – USA; *R. nigrum* – China; *Ribes* sp. – USA.

Notes – In the phylogenetic tree (Fig. 1A), *C. ribis-taedae* is phylogenetically sister to *C. ribicola* and *C. peridiatum*, but differs from these two allied species in ornamentation of aeciospores and the dimension of teliospores (Fig. 15). Host alternation of *C. ribis-taedae* was found between *P. taeda* and *R. nigrum* (Table 2).

Cronartium sahoanum (Imazu & Kakish.) Aime & Rossman. IMA Fungus 9(1): 82. 2018.

MycoBank number: MB824648

Synonym – *Endocronartium sahoanum* Imazu & Kakish., in Imazu, Kakishima & Kaneko, Trans. Mycol. Soc. Japan 30(3): 308. 1989.

Spermogonia formed between periderm and cortex of stems, indeterminate in growth, hymenia flat. Telia intracortical in origin, erumpent with developed peridia, teliospores catenulate, broadly ellipsoid, subglobose or obovoid, 24–42 × 17–31 µm, walls hyaline, verrucose, 2–3 µm thick, warts on spores annulate, 5–6 annuli. Basidia external.

Type – Japan, Iwate prefecture, Mokkodake, Mt. Hachimantai, Matsuo-mura, Iwate-gun, 0, III on *P. pumila*, 16 Jun 1987, M. Imazu, TSH-R526 (holotype).

Host and geographical distribution confirmed in this study – *P. pumila* – Japan.

Notes – Imazu et al. (1989) described a species on *P. pumila* in Japan as *Endocronartium sahoanum*. Later, Aime et al. (2018b) transferred this species to *Cronartium*. Sequence data was not available from this species, and we temporarily treat it as an independent species due to its *Peridermium*-type telia on *Pinus*.

Cronartium strobilinum (Arthur) Hedgc. & G. Hahn, Phytopathology 12: 113. 1922.

Synonyms – *Caeoma strobilinum* Arthur, Bull. Torrey Bot. Club 33: 519. 1906.

Peridermium strobilinum (Arthur) R.S. Peterson, Bull. Torrey Bot. Club 94: 537. 1967.

Spermogonia not found. Aecia on cones, brown or black, peridia not easily detected, aeciospores ellipsoid, obovoid, or subglobose, 22–36 × 13–17 µm, wall 2.0–4.0 µm thick including verrucae connected by filaments, verrucae 1.4–2.5 µm high, nailhead-like verrucae with 3–5 annuli. Uredinia hypophyllous, occasionally epiphyllous, subepidermal, with bright peridia, forced up to dome, urediniospores globoid, ellipsoid or ovoid, 14–27 × 11–18 µm, wall 1.5–3 µm thick, echinulate, germ pores mostly scattered, inconspicuous. Telia hypophyllous, arising from the center of uredinia, cylindrical, mostly curved, up to 6 mm long, 85–180 µm wide, teliospores oblong or cylindrical, cross-section of telia with 6–10 teliospores, 23–49 × 10–18 µm, walls smooth, 2.5–5.0 µm thick. Basidia external.

Material examined – USA, Florida, 0, I on *P. caribaea*, 16 Apr 1939, West & DeVall, FLAS-F-22755; USA, Florida, 0, I on *P. taeda*, 10 Jun 1982, S. Gilly, FLAS-F-53222; USA, Florida, III on *Q. geminata*, 20 Mar 1940, G.G. Hedgcock, FLAS-F-45215; USA, Florida, III on *Q. laurifolia*, 13 Sept 1925, A.S. Rhoads, FLAS-F-07030; USA, Florida, III on *Q. minima*, 6 Jan 1940, G.G. Hedgcock, FLAS-F-45244; USA, Florida, III on *Q. myrtifolia*, 7 May 1920, A.S. Rhoads, FLAS-F-25395; USA, Florida, III on *Q. virginiana*, 23 Apr 1926, A.S. Rhoads, FLAS-F-25398.

Hosts and geographical distribution confirmed in this study – *P. caribaea* – Cuba, USA; *P. elliottii var. densa* – Cuba, USA; *P. taeda* – USA; *Q. alba* – USA; *Q. geminata* – USA; *Q. laurifolia* – USA; *Q. minima* – USA; *Q. myrtifolia* – USA; *Q. minima* – USA; *Q. virginiana* – USA.

Notes – Arthur (1906) described a rust fungus on cones of *P. heterophylla* in Florida, USA as *Caeoma strobilina*. Later, inoculation experiments confirmed its telial stage on several oak species, and Hedgecock & Hunt (1922) proposed a new combination, *Cronartium strobilinum*. This species differs from other oak rusts, i.e., *C. fusiforme*, *C. mongolicum*, *C. orientale* and *C. quercuum*, in its aecia on the cone and unique character of uredinia with peridial cells. In addition, it differs from *C. fusiforme* and *C. orientale* in the dimension of aeciospores (22–36 × 13–17 µm vs 17–45 × 15–27 µm vs 18–25 × 13–22 µm). This species occurs in several countries in the American continent, and more attention needs to be paid to this disease due to its high potential threat to Asian and European pine plantations.

Cronartium yamabense (Saho & I. Takah.) Aime & Rossman, in Aime, et al., IMA Fungus 9(1): 82. 2018.

Synonyms – *Peridermium yamabense* Saho & I. Takah., in Saho, Trans. Mycol. Soc. Japan 22(1): 33. 1981.

Endocronartium yamabense (Saho & I. Takah.) Paclt, Mitt. Dtsch. Dendrol. Ges. 77: 227. 1987.

Spermogonia formed between periderm and cortex of stems, indeterminate in growth, hymenia flat. Telia intracortical in origin, erumpent with developed peridia, teliospores catenulate, broadly ellipsoid, subglobose or obovoid, 23–40 × 16–31 µm, walls hyaline, verrucose, 2–3 µm thick, warts on spores longitudinal ditch-like, verrucae with 1 annulus. Basidia external.

Material examined – Japan, Toyama prefecture, Raichozawa, Mt. Tateyama, 0, III on *P. pumila*, 6 Aug 1960, M. Imazu, TSH-R12758.

Host and geographical distribution confirmed in this study – *P. pumila* – Japan.

Notes – Saho (1981) recognized *Cronartium* on twigs of *P. pumila* in Japan as a new pine-to-pine (autoecious) species and named it *Per. yamabense*. Later, Imazu & Kakishima (1992) found that it was an endocyclic species having spermogonia and telia on pines, and thus named it as *Endocronartium yamabense*. Later Aime et al. (2018b) transferred this to *Cronartium*, as *C. yamabense*. Because of its unique telial morphology, we treat this species as an independent species.

Discussion

Cronartium species recognition and their taxonomic criteria

Within *Cronartium*, species recognition was previously exclusively based on morphology, but the taxonomic importance of morphological features in different parts of the entire life cycle varies at different taxonomic ranks. Among the spore states, spermogonia are usually not easily detected in preserved specimens although there are distinct morphological variations in the shape and size of spermatia of different species (Hiratsuka et al. 1992). On aecial hosts, ornamentation, shape, and size of aeciospores and peridial cells have long been used for species recognition (Peterson 1967, Hiratsuka 1971). On telial hosts, ornamentation, shape, and size of urediniospores and teliospores serve as important criteria for species recognition (Peterson 1967, 1974, Cummins & Hiratsuka 2003). In addition, the size and color of basidia and basidiospores were occasionally used to differentiate cryptic species (Kaneko 2000). However, due to lack of life cycle information, morphology on aecial and telial hosts were used independently for species recognition, which led to confusion with unnecessary names introduced in the genus *Cronartium* (Peterson 1967, 1974). With the aid of molecular data, connection of aecia and telia provides additional characters for species recognition, especially for those that share similar morphology in one spore stages. Morphological characteristics in both aecia and telia, especially the ultrastructure of spore ornamentation and peridial cells, seem to be useful in delimitation of *Cronartium* species. Although the type of life cycle, e.g., endocyclic life cycle, was once considered an important criterion, the separation of several species into different genera based on the type of life cycle has long been questioned (Laundon 1976, Hiratsuka 1995, Vogler & Bruns 1998). In our studies, we have confirmed that endo-type life cycle is not an effective character for species recognition because several species with endo-type life cycle are conspecific to certain *Cronartium* species.

Taxonomic results serve for quarantine purpose

Cronartium species are one of the most damaging pathogens in forestry, and several species, such as *C. coleosporioides*, *C. comandrae*, *C. comptoniae*, *C. conigenum*, *C. flaccidum*, *C. fusiforme*, *C. quercuum* and *C. ribicola*, are listed as important inspection targets in many north hemisphere countries (EPPO 2019, 2021). Among these quarantine pathogens, the delimitation of several species, i.e., *C. coleosporioides*, *C. comandrae*, *C. quercuum*, *C. ribicola*, has long been in a state of disorder, so that recognition between morphologically similar species was impossible due to their unclear species boundaries. For quarantine and inspection, the US treated all species in *Cronartiacae* as the target. In the European Union, seven *Cronartium* species (*C. coleosporioides*, *C. comandrae*, *C. comptoniae*, *C. fusiforme*, *C. harknessii*, *C. himalayense* and *C. quercuum*) are in the A1 quarantine list, and *C. kamtschaticum* is in the A2 list. Through our studies, we have determined that *C. fusiforme* should not be included in the A1 list as it is distributed in several countries in the EU. In China, six *Cronartium* species, i.e. *C. coleosporioides*, *C. comandrae*, *C. conigenum*, *C. fusiforme*, *C. harknessii*, and *C. ribicola* are now listed as quarantine pathogens (Duan et al. 2017). We confirmed the geographic distribution and host alternation of those species, and *C. coleosporioides*, *C. comandrae*, *C. conigenum*, *C. fusiforme* and *C. harknessii* should be treated as quarantine pathogens in China. In addition, other important pathogens, such as *C. arizonicum*, *C. comptoniae*, *C. pyriforme*, *C. quercuum*, *C. strobilinum*, should be added to the Chinese quarantine list due to their potential threats to pine forests. Moreover, our previous studies in quarantine fungi of *Dothideomycetes* (Zhao et al. 2021b) and current studies have emphasized the necessity of reconsidering the list of Chinese quarantine pests.

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