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Phylogeny and taxonomy of *Ophiognomonia* (Gnomoniaceae, Diaporthales), including twenty-five new species in this highly diverse genus

Donald M. Walker · Lisa A. Castlebury · Amy Y. Rossman · Luis C. Mejía · James F. White

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Abstract Species of *Ophiognomonia* are leaf-inhabiting endophytes, pathogens, and saprobes that infect plants in the families Betulaceae, Fagaceae, Juglandaceae, Lauraceae, Malvaceae, Platanaceae, Rosaceae, Salicaceae, and Sapindaceae. Based on extensive collecting, this species-rich genus is now known to have a world wide distribution in primarily temperate areas, although some species are known from the subtropics. Analyses of DNA sequences from three markers including guanine nucleotide-binding protein subunit beta-like protein (MS204), translation elongation factor 1α (*tef-1α*), and the ITS region including ITS1, 5.8 S rDNA and ITS2 regions (ITS) were used to define phylogenetic species in *Ophiognomonia.* Host plant association correlated with these species. Twenty-five new species of *Ophiognomonia* and two new combinations are proposed with descriptions and illustrations. In addition, descriptions and illustrations are provided for 12 other species of *Ophiognomonia*. A key is provided to the 45 currently accepted species of *Ophiognomonia.* The disposition of additional names in *Ophiognomonia* is also discussed.

Keywords Birch foliar pathogen · Butternut canker · GCPSR · Genealogical sorting index · Host associations · MS204 · Multilocus phylogeny · Walnut anthracnose and leaf blotch

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Introduction

Fungi in the family Gnomoniaceae (Diaporthales, Sordariomycetes, Ascomycota) are associated with a diverse range of herbaceous plants, shrubs, and trees from over 330 host genera in North America and Europe (Farr, D.F. & Rossman, A.Y. Fungal Databases, Systematic Mycology and Microbiology Laboratory, ARS, USDA. Retrieved September 19, 2011, from http://nt.ars-grin.gov/fungaldatabases/) and function in the environment as endophytes, pathogens, and saprobes. Recently nine genera were recognized in a comprehensive monograph of the Gnomoniaceae (Sogonov et al. 2008). These nine genera were identified on the basis of a three-marker phylogeny based on the 5′ region of the large ribosomal subunit (nrLSU) and exons from the translation elongation factor 1-alpha (*tef-1α)* and RNA polymerase II (*rpb2*) genes. Mejía et al. (2011a) increased the number of gnomoniaceous genera to ten by describing the monotypic genus *Occultocarpon,* which occurs on *Alnus nepalensis* in China. Although the modern genera of Gnomoniaceae have been defined by DNA sequence data, other characters such as host association, presence/absence of stroma, and perithecial habit are also important (Sogonov et al. 2008). For example,

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the genus *Cryptosporella* produces perithecia aggregated in stromata on twigs, whereas the perithecia of *Gnomonia* are solitary and erumpent on overwintered leaves.

The purpose of this study is to document species diversity in the genus *Ophiognomonia* using multiple molecular markers. *Ophiognomonia* has a worldwide distribution, primarily in temperate forests, but with a few species that occur in subtropical regions, and is based on the type species *O. melanostyla* (DC. : Fr.) Berl. found on *Tilia* spp. in temperate forests in USA and Europe. Sogonov et al. (2008) recognized 17 species in the genus *Ophiognomonia* on host plants in the Betulaceae, Fagaceae, Juglandaceae, Lauraceae, Malvaceae, Platanaceae, Rosaceae, Salicaceae, and Sapindaceae. Historically, knowledge of geographic distribution and host association of species in this genus was limited, especially in Asia and South America. Kobayashi (1970) collected a single species, *O. setacea* as *Gnomonia setacea* on *Quercus* in Japan. Otani (1995) observed *O. leptostyla* on *Juglans* sp. and *O. setacea* on *Castanea* sp. and *Quercus* sp. from Japan. Reports and collections of *Ophiognomonia* from Europe and North America are more common than in Asia, but are still somewhat limited. For example, Barr (1978) accepted a single species, *O. melanostyla* on *Tilia* sp. from Europe and the United States. Monod (1983) described eight additional species distributed throughout Europe and North America.

Species of *Ophiognomonia* cause diseases of economically important hardwood trees, including *O. intermedia* (Rehm) Sogonov with the asexual state *Discula betulae* (Westend.) Pennycook, which causes a foliar disease of birch and dieback of young shoots (Green 2004; Green and Castlebury 2007; Pennycook 2007). Walnut anthracnose and leaf blotch are caused by virulent strains of *Ophiognomonia leptostyla* in the eastern half of the United States, South America, Europe, and Asia (Neely and Black 1976; Berry 1981; Juhasova et al. 2006; Belisario et al. 2008). Disease epidemics caused by *O. leptostyla* are particularly destructive during the rainy and cool seasons in Iran, which is the third highest walnut producer in the world (Behdad 1991; Belisario et al. 2008; Salahi et al. 2009). Perhaps the most devastating member of the genus in North America is the asexually reproducing *O. clavigignenti-juglandacearum* (Nair, Kostichka, & Kuntz) Broders & Boland, which causes butternut canker (*Juglans cinerea* L.) with past reports documenting 70–90 % tree decline in some areas (Anderson and LaMadeleine 1978; Broders and Boland 2011).

Prior to Sogonov et al. (2008) considerable confusion existed about the generic concept of *Ophiognomonia*. *Ophiognomonia melanostyla* was originally described in the genus *Sphaeria* and then transferred to *Cryptoderis*, *Gnomonia,* and *Gnomoniella* before being designated as the type species of *Ophiognomonia* in 1899 (see Sogonov et al. 2008). Many species now in *Ophiognomonia* were scattered amongst various gnomoniaceous genera due to emphasis of differing morphological characters by different authors. For many years considerable importance was placed on the shape and septation of ascospores. For example, Monod (1983) included both *O. rubi-idaei* (M. Monod) Sogonov and *O. trientensis* (M. Monod) Sogonov in *Gnomonia* based on the short, ellipsoidal, one-septate ascospores. Barr (1978) emphasized placement of the perithecial neck thus recognizing *Plagiostoma micromegala* (Ellis & Everh.) M.E. Barr and *Pleuroceras sassafras* (Ellis & Everh.) M.E. Barr, now both included in *Ophiognomonia* (Sogonov et al. 2008).

Within the Gnomoniaceae species are based on the phylogenetic analyses of molecular markers. Host association and morphological characters such as ascospore size and septation can also be useful for species identification. Recent phylogenetic studies have shown that species of Gnomoniaceae often have a narrow host range associating with a single host genus or species (Mejía et al. 2008, 2011a, b, c; Sogonov et al. 2008; Walker et al. 2010). For example, in the genus *Cryptosporella* nine species are associated with a single host species or subspecies and seven fungal species occur on a single host genus (Mejía et al. 2011b). Mejía et al. (2011b) suggest that the genus *Cryptosporella* has undergone speciation within the geographic host ranges of Betulaceae, Fagaceae, and Salicaceae. Walker et al. (2010) used ascospore size, septation, and host association to supplement phylogenetic recognition of species in the genus *Gnomoniopsis.* Four species of *Gnomoniopsis* are specific to the host genus *Rubus* and ten additional species associate with nine other host genera in the Fagaceae, Onagraceae, and Rosaceae.

Based on theory from Avise and Ball (1990), Taylor et al. (2000) coined genealogical concordance phylogenetic species recognition (GCPSR) as an approach for defining fungal species based on congruent gene trees. Seven genes in various combinations have been commonly used for GCPSR of fungi, specifically nuclear large and small ribosomal subunits, 5.8 S ribosomal RNA gene, subunits 1 and 2 of RNA polymerase II, *tef-lα*, and mitochondrial ATP synthase as well as the nuclear ribosomal internal transcribed spacer (ITS) regions 1 and 2 (e.g., Damm et al. 2007; Letcher et al. 2008; Mejía et al. 2011b; Raja et al. 2008; Spatafora et al. 2006; Walker et al. 2010). As fungal genomic data became available, additional molecular markers were added to the mycologist's toolbox (Aguileta et al. 2008; Schmitt et al. 2009; Walker et al. 2012) but it can be difficult to evaluate species limits and the contribution and usefulness of the individual genes in a phylogenetic analysis. More recently the genealogical sorting index (*gsi*; Cummings et al. 2008) has been used to quantify exclusivity

of ancestry of monophyletic groups. Phylogenetic informativeness profiles incorporate nucleotide substitution rates over evolutionary time and can assist in marker selection for phylogenetic questions (Townsend 2007). Walker et al. (2012) applied phylogenetic informativeness (Townsend 2007; Townsend and Leuenberger 2011) to assess the usefulness of five molecular markers including *β-tubulin*, FG1093 (60 S ribosomal protein L37), ITS, MS204 (guanine nucleotide-binding protein subunit beta-like protein), and *tef-1α,* in resolving lower-level relationships in *Ophiognomonia* and determined that concatenation of ITS, MS204, and *tef-1α* accurately represent the topology of the combined five-marker dataset.

DNA sequences from three ribosomal DNA and protein coding molecular markers, namely MS204, *tef-1α*, and ITS are used in this study to determine the species diversity of *Ophiognomonia*. Monophyletic species are evaluated using GCPSR and *gsi* in single and combined-marker genealogies. Twenty-five new species of *Ophiognomonia* and two new combinations are proposed with descriptions and illustrations. In addition, descriptions and illustrations are provided for the 12 combinations included without description in Sogonov et al. (2008). A key is provided to the 45 currently accepted species of *Ophiognomonia.*

Methods

Morphological observations

Macroscopic and microscopic characters were observed and digital images captured as in Walker et al. (2010). Freshly collected specimens were isolated and grown in culture according to Walker et al. (2010). Freshly collected specimens determined as immature due to lack of ascospore germination in culture were placed in moist chambers. The moist chambers were airtight plastic boxes/bags with moist paper towels lining the bottom surface. They were placed at 4 °C in complete darkness and observed weekly for ascospore maturation and germination in culture. Cultures were deposited at the Centraalbureau voor Schimmelcultures (CBS) in the Netherlands (Table 1).

DNA extraction, amplification, and sequencing

Cultures were grown and genomic DNA extracted using the QIAGEN Puregene Core Kit A (QIAGEN Inc., Chatsworth, California) as in Walker et al. (2010). The markers ITS, MS204, and *tef-1α* were selected for analysis based on phylogenetic informativeness test results from Walker et al. (2012). ITS and *tef-1α* were amplified and sequenced according to Walker et al. (2010) with the addition of four gnomoniaceae-specific *tef-1α* primers designed in Walker et al. (2012). The marker MS204 was amplified and sequenced as in Walker et al. (2012).

Sequence data analyses

Raw sequences were edited and assembled into contigs with Sequencher 4.9 for Windows (Gene Codes Corp., Ann Arbor, Michigan). Eight alignments were prepared using the MAFFT v.6 web server (http://mafft.cbrc.jp/alignment/server/) and curated with the Gblocks (Castresana 2000; Talavera and Castresana 2007) web server (http://molevol.cmima.csic.es/castresana/Gblocks_server.html). The alignment strategy for each marker was set at L-INS-i for nucleotide sequences in MAFFT v.6. Manual alignment modifications were performed before running Gblocks with the default parameters. Alignments one, two, and three correspond to the markers ITS, *tef-1α,* and MS204, respectively. Each alignment was composed of DNA sequences for 45 isolates, representing 43 species in *Ophiognomonia* and the outgroup taxa *Ambarignomonia petiolorum* and *Discula destructiva* in the Gnomoniaceae. The three individually aligned sequence markers were concatenated into a single file to form alignment four. Alignments 5–7 correspond to combined three-marker alignments for three independently supported clades of species within *Ophiognomonia.* Each marker was aligned individually as previously mentioned, then concatenated to form a single file for each of the three clades. Alignment five (clade one) consisted of 39 isolates, representing 15 species in *Ophiognomonia,* and the outgroup taxon *O. longispora*. Alignment six (clade two) consisted of 25 isolates, representing 11 species in *Ophiognomonia,* and the outgroup *O. monticola*. Alignment seven (clade three) consisted of 35 isolates, representing 15 species in *Ophiognomonia,* and the outgroup taxa *O. gei-montani* and *O. leptostyla*. Alignment eight consisted of ITS sequences from the same 25 isolates in alignment six, plus four additional ITS sequences representing two species of *Ophiognomonia* lacking a culture, for a total of 29 ITS sequences representing 13 species of *Ophiognomonia* and the outgroup *O. monticola.*

Potential conflict among datasets was assessed by comparing the three individual gene trees across all alignments with a conditional comparison test using maximum parsimony bootstrap (MPBS) analyses with a cutoff value of ≥70 % for a supported clade (Mason-Gamer and Kellogg 1996; Kellogg et al. 1996; Johnson and Soltis 1998). Phylogenetic trees were inferred with maximum parsimony (MP), maximum likelihood (ML), and Bayesian analyses. In all analyses rooting was accomplished with the outgroup method (Nixon and Carpenter 1993) using results from this study and from Sogonov et al. (2008). For MP analyses each gene was analyzed individually and then together in a three-marker combined alignment using PAUP 4.0b10 (Swofford 2002) according to Walker et al. (2010). The University of

Table 1 Specimens and cultures of Gnomoniaceae sequenced for this study

Species	CBS #	Isolate	Specimen	ITS	MS204	*tef1-α*	Country	Host	Collector
Ambarignomonia petiolorum	CBS 121227	AR 4082	BPI 844274	EU254748.1*	JQ414056	JQ414140	USA	*Liquidambar styraciflua*	M.V. Sogonov
Discula destructiva	CBS 109771	AR 2596	BPI 1107757	JQ414221	JQ414053	JQ414137	USA	*Cornus nuttallii*	S. Redlin
Ophiognomonia alni-cordatae	CBS 131353	DMW 384.1	BPI 882233	JQ414243	JQ414091	JQ414175	Japan	*Alnus cordata*	D.M. Walker
Ophiognomonia alni-viridis	CBS 782.79	CBS 782.79	NA	EU254864.1*	JQ414064	JQ414148	Switzerland	*Alnus viridis*	M. Monod
Ophiognomonia alni-viridis	CBS 783.79	CBS 783.79	NA	EU254865.1*	JQ414065	JQ414149	Switzerland	*Betula* sp.	M. Monod
Ophiognomonia alni-viridis	CBS 131408	DMW 439.3	BPI 882251	JQ414260	JQ414108	JQ414192	USA	*Betula* sp.	D.M. Walker
Ophiognomonia alni-viridis	CBS 128358	LCM 494	BPI 879541	JF514848*	JF319085*	JF514826*	USA	*Alnus sinuata*	L.C. Mejía
Ophiognomonia apiospora	CBS 131425	LCM 503.05	BPI 879601	JQ414286	JQ414134	JQ414218	China	*Alnus nepalensis*	L.C. Mejía
Ophiognomonia apiospora	CBS 131426	LCM 503.06	BPI 879601	JQ414287	JQ414135	JQ414219	China	*Alnus nepalensis*	L.C. Mejía
Ophiognomonia asiatica	CBS 131351	DMW 378.2	BPI 882231	JQ414241	JQ414089	JQ414173	Japan	*Quercus serrata*	D.M. Walker
Ophiognomonia asiatica	CBS 131345	DMW 351.3	BPI 882220	JQ414233	JQ414081	JQ414165	Japan	*Quercus serrata*	D.M. Walker
Ophiognomonia asiatica	CBS 131347	DMW 361.1	BPI 882225	JQ414236	JQ414084	JQ414168	Japan	*Quercus aliena*	D.M. Walker
Ophiognomonia asiatica	CBS 131424	LCM 500.01	BPI 879600	JQ414285	JQ414133	JQ414217	China	*Quercus* sp.	L.C. Mejía
Ophiognomonia balsamiferae	CBS 121266	AR 4320	BPI 877606	EU254870.1*	JF319077*	JF514827*	Canada	*Populus balsamifera*	M.V. Sogonov
Ophiognomonia bugabensis	NA	LCM 362	NA	JQ414283	JQ414131	JQ414215	Panama	*Alnus acuminata*	L.C. Mejía
Ophiognomonia bugabensis	CBS 131399	LCM 368	NA	JQ414284	JQ414132	JQ414216	Panama	*Alnus acuminata*	L.C. Mejía
Ophiognomonia clavigignenti-juglandacearum	CBS 121081	AR 3791	NA	DQ323533.1*	JQ414054	JQ414138	USA	*Juglans cinerea*	M. Ostry
Ophiognomonia clavigignenti-juglandacearum	NA	AR 4539	NA	JQ414222	JQ414061	JQ414145	USA	*Juglans cinerea*	S. Anagnostakis
Ophiognomonia clavigignenti-juglandacearum	NA	ATCC 36624	BPI 880702	EU255069.1*	JQ414062	JQ414146	USA	*Juglans cinerea*	V.M.G. Nair
Ophiognomonia cordicarpa	CBS 131342	DMW 344.2	BPI 882217	JQ414230	JQ414078	JQ414162	Japan	*Pterocarya rhoifolia*	D.M. Walker
Ophiognomonia gardiennetii	CBS 131409	DMW 442.1	BPI 882252	JQ414261	JQ414109	JQ414193	USA	*Alnus serrulata*	D.M. Walker
Ophiognomonia gardiennetii	CBS 131417	DMW 469.3	BPI 882262	JQ414265	JQ414113	JQ414197	USA	*Alnus serrulata*	D.M. Walker
Ophiognomonia gardiennetii	CBS 131429	DMW 513.1	BPI 882276	JQ414269	JQ414117	JQ414201	USA	*Alnus serrulata*	D.M. Walker
Ophiognomonia gei	CBS 818.79	CBS 818.79	NA	EU254928.1*	NA	NA	Switzerland	*Fragaria vesca*	M. Monod
Ophiognomonia gei-montani	CBS 821.79	CBS 821.79	NA	EU254871*	JF319078*	JF514828*	Switzerland	*Geum montanum*	M. Monod
Ophiognomonia gunmensis	CBS 131401	DMW 388.1	BPI 882236	JQ414246	JQ414094	JQ414178	Japan	*Quercus serrata*	D.M. Walker
Ophiognomonia hiawathae	CBS 131413	DMW 458.3	BPI 882256	JQ414263	JQ414111	JQ414195	USA	*Betula lutea*	D.M. Walker
Ophiognomonia hiawathae	CBS 131416	DMW 466.1	BPI 882261	JQ414264	JQ414112	JQ414196	USA	*Betula lutea*	D.M. Walker
Ophiognomonia ibarakiensis	CBS 131405	DMW 419.3	BPI 882247	JQ414257	JQ414105	JQ414189	Japan	*Alnus* sp.	D.M. Walker
Ophiognomonia ibarakiensis	CBS 131349	DMW 371.1	BPI 882227	JQ414238	JQ414086	JQ414170	Japan	*Alnus* sp.	D.M. Walker
Ophiognomonia intermedia	CBS 119197	AR 4147	BPI 880534	EU254875.1*	JF319074*	JF514825*	United Kingdom	*Betula alba*	S. Green
Ophiognomonia intermedia	CBS 131421	DMW 486.1	BPI 882267	JQ414267	JQ414115	JQ414199	USA	*Betula lutea*	D.M. Walker
Ophiognomonia intermedia	CBS 131418	DMW 470.1	BPI 882263	JQ414266	JQ414114	JQ414198	USA	*Alnus serrulata*	D.M. Walker
Ophiognomonia ischnostyla	CBS 121234	AR 4190	BPI 871054B	EU254897.1*	JQ414058	JQ414142	Switzerland	*Corylus avellana*	M.V. Sogonov

Table 1 (continued)

Species	CBS #	Isolate	Specimen	ITS	MS204	*tef1-α*	Country	Host	Collector
Ophiognomonia ischnostyla	CBS 838.79	CBS 838.79	NA	EU254891.1*	JQ414066	JQ414150	Switzerland	*Carpinus betulus*	M. Monod
Ophiognomonia japonica	CBS 131355	DMW 387.2	BPI 882235	JQ414245	JQ414093	JQ414177	Japan	*Prunus japonica*	D.M. Walker
Ophiognomonia kobayashii	CBS 131343	DMW 347.2	BPI 882218	JQ414231	JQ414079	JQ414163	Japan	*Castanea crenata*	D.M. Walker
Ophiognomonia kobayashii	CBS 131352	DMW 379.3	BPI 882232	JQ414242	JQ414090	JQ414174	Japan	*Castanea crenata*	D.M. Walker
Ophiognomonia kobayashii	CBS 131350	DMW 374.2	BPI 882229	JQ414240	JQ414088	JQ414172	Japan	*Castanea crenata*	D.M. Walker
Ophiognomonia kobayashii	CBS 131403	DMW 416.1	BPI 882245	JQ414255	JQ414103	JQ414187	Japan	*Castanea crenata*	D.M. Walker
Ophiognomonia lenticulispora	CBS 131363	DMW 544	BPI 882287	JQ414277	JQ414125	JQ414209	USA	*Prunus* sp.	D.M. Walker
Ophiognomonia leptostyla	CBS 110136	CBS 110136	NA	DQ323535.1*	JQ414063	JQ414147	USA	*Juglans* sp.	D. Farr
Ophiognomonia longispora	CBS 131337	DMW 325.4	BPI 882210	JQ414225	JQ414073	JQ414157	Japan	*Tilia maximowicziana*	D.M. Walker
Ophiognomonia longispora	CBS 131358	DMW 394.3	BPI 882239	JQ414249	JQ414097	JQ414181	Japan	*Tilia maximowicziana*	D.M. Walker
Ophiognomonia maximowiczianae	CBS 131357	DMW 392.1	BPI 882238	JQ414248	JQ414096	JQ414180	Japan	*Betula maximowicziana*	D.M. Walker
Ophiognomonia melanostyla	CBS 131431	DMW 533	BPI 882279	JQ414270	JQ414118	JQ414202	France	*Tilia* sp.	Y. Mourgues, M. Chovillon
Ophiognomonia melanostyla	CBS 128482	LCM 389.01	BPI 879257	JF514849*	JF319084*	JF514830*	Germany	*Tilia heterophylla*	L.C. Mejía
Ophiognomonia michiganensis	CBS 131412	DMW 454.3	BPI 882255	JQ414262	JQ414110	JQ414194	USA	*Betula papyrifera*	D.M. Walker
Ophiognomonia michiganensis	CBS 131422	DMW 492.1	BPI 882268	JQ414268	JQ414116	JQ414200	USA	*Alnus serrulata*	D.M. Walker
Ophiognomonia michiganensis	CBS 121252	AR 4295	BPI 877624	EU254901.1*	JF319076*	JF514820*	USA	*Betula lenta*	M.V. Sogonov
Ophiognomonia micromegala	CBS 131432	DMW 535	BPI 882280	JQ414271	JQ414119	JQ414203	USA	*Carya* sp.	D.M. Walker
Ophiognomonia micromegala	CBS 131433	DMW 536	BPI 882281	JQ414272	JQ414120	JQ414204	USA	*Carya* sp.	D.M. Walker
Ophiognomonia monticola	CBS 131346	DMW 357.3	BPI 882222	JQ414235	JQ414083	JQ414167	Japan	*Carpinus* sp.	D.M. Walker
Ophiognomonia monticola	CBS 131361	DMW 405.3	BPI 882243	JQ414253	JQ414101	JQ414185	Japan	*Carpinus* sp.	D.M. Walker
Ophiognomonia multirostrata	CBS 131348	DMW 364.3	BPI 882226	JQ414237	JQ414085	JQ414169	Japan	*Alnus firma*	D.M. Walker
Ophiognomonia multirostrata	CBS 131400	DMW 373.1	BPI 882228	JQ414239	JQ414087	JQ414171	Japan	*Alnus firma*	D.M. Walker
Ophiognomonia multirostrata	CBS 131406	DMW 423.1	BPI 882248	JQ414258	JQ414106	JQ414190	Japan	*Alnus firma*	D.M. Walker
Ophiognomonia naganoensis	CBS 131338	DMW 331.2	BPI 882211	JQ414226	JQ414074	JQ414158	Japan	*Alnus hirsuta var. sibirica*	D.M. Walker
Ophiognomonia naganoensis	CBS 131362	DMW 410.1	BPI 882244	JQ414254	JQ414102	JQ414186	Japan	*Alnus hirsuta var. sibirica*	D.M. Walker
Ophiognomonia naganoensis	CBS 131404	DMW 418.3	BPI 882246	JQ414256	JQ414104	JQ414188	Japan	*Alnus hirsuta*	D.M. Walker
Ophiognomonia nana	CBS 883.79	CBS 883.79	NA	JQ414223	JQ414071	JQ414155	Finland	*Betula nana*	M. Monod
Ophiognomonia nipponicae	CBS 131407	DMW 424.1	BPI 882249	JQ414259	JQ414107	JQ414191	Japan	*Prunus nipponica*	D.M. Walker
Ophiognomonia ostryae-virginianae	CBS 131398	LCM 155.01	BPI 879596	JQ414282	JQ414130	JQ414214	USA	*Ostrya virginiana*	L.C. Mejía
Ophiognomonia otanii	CBS 131402	DMW 401.3	BPI 882242	JQ414252	JQ414100	JQ414184	Japan	*Castanea crenata*	D.M. Walker
Ophiognomonia otanii	CBS 131354	DMW 385.1	BPI 882234	JQ414244	JQ414092	JQ414176	Japan	*Castanea crenata*	D.M. Walker
Ophiognomonia otanii	CBS 131356	DMW 390.1	BPI 882237	JQ414247	JQ414095	JQ414179	Japan	*Castanea crenata*	D.M. Walker
Ophiognomonia otanii	CBS 131360	DMW 397.1	BPI 882241	JQ414251	JQ414099	JQ414183	Japan	*Castanea crenata*	D.M. Walker
Ophiognomonia padicola	CBS 845.79	CBS 845.79	NA	JF514845*	JF319080*	JF514832*	Switzerland	*Prunus padus*	M. Monod
Ophiognomonia pseudoclavulata	CBS 121236	AR 4059	BPI 844280	EU254923.1*	JF319073*	JF514819*	USA	*Carya tomentosa*	M.V. Sogonov

Table 1 (continued)

Species	CBS #	Isolate	Specimen	ITS	MS204	*tef1-α*	Country	Host	Collector
Ophiognomonia pseudoclavulata	CBS 131434	DMW 538	BPI 882283	JQ414273	JQ414121	JQ414205	USA	*Carya* sp.	D.M. Walker
Ophiognomonia pseudoclavulata	CBS 131367	DMW 551	BPI 882290	JQ414280	JQ414128	JQ414212	USA	*Carya* sp.	D.M. Walker
Ophiognomonia pseudoischnostyla	CBS 121228	AR 4120	BPI 877616	EU254919.1*	JQ414057	JQ414141	Russia	*Betula pubescens*	M.V. Sogonov
Ophiognomonia pseudoischnostyla	CBS 842.79	CBS 842.79	NA	EU254892.1*	JQ414067	JQ414151	Switzerland	*Alnus incana*	M. Monod
Ophiognomonia pterocaryae	CBS 131359	DMW 396.3	BPI 882240	JQ414250	JQ414098	JQ414182	Japan	*Pterocarya rhoifolia*	D.M. Walker
Ophiognomonia pterocaryae	CBS 131344	DMW 350.2	BPI 882219	JQ414232	JQ414080	JQ414164	Japan	*Pterocarya rhoifolia*	D.M. Walker
Ophiognomonia quercus-gambellii	CBS 131397	DMW 117.1	BPI 882202	JQ414224	JQ414072	JQ414156	USA	*Quercus kellogii*	D.M. Walker
Ophiognomonia rosae	CBS 850.79	CBS 850.79	NA	EU254929.1*	JQ414068	JQ414152	Switzerland	*Rubus* sp.	M. Monod
Ophiognomonia rosae	CBS 851.79	CBS 851.79	NA	EU254930.1*	JQ414069	JQ414153	Finland	*Comarum palustre*	M. Monod
Ophiognomonia rosae	CBS 128442	DMW 108.2	BPI 882201	JF514851*	JF319081*	JF514824*	USA	*Fragaria vesca*	D.M. Walker
Ophiognomonia rosae	CBS 131365	DMW 543	BPI 882286	JQ414276	JQ414124	JQ414208	France	*Rubus* sp.	A. Gardiennet
Ophiognomonia rubi-idaei	NA	NA	BPI 877559B	EU254939.1*	NA	NA	Canada	*Rubus* sp.	M.V. Sogonov
Ophiognomonia rubi-idaei	NA	NA	BPI 877637	EU254937.1*	NA	NA	Switzerland	*Rubus ideaus*	M.V. Sogonov
Ophiognomonia rubi-idaei	NA	NA	BPI 877638	EU254938.1*	NA	NA	Canada	*Rubus spectabilis*	M.V. Sogonov
Ophiognomonia sassafras	CBS 121243	AR 4284	BPI 877639	EU254941.1*	JF319075*	JF514829*	USA	*Sassafras albidum*	M.V. Sogonov
Ophiognomonia sassafras	CBS 131435	DMW 541	BPI 882284	JQ414274	JQ414122	JQ414206	USA	*Sassafras albidum*	C.M. Milensky
Ophiognomonia sassafras	CBS 131366	DMW 542	BPI 882285	JQ414275	JQ414123	JQ414207	USA	*Sassafras albidum*	D.M. Walker
Ophiognomonia setacea	CBS 121230	AR 4193	BPI 877646	EU254955.1*	JQ414059	JQ414143	USA	*Castanea dentata*	M.V. Sogonov
Ophiognomonia setacea	CBS 859.79	CBS 859.79	NA	AY818958.1*	JQ414070	JQ414154	Switzerland	*Quercus* sp.	M. Monod
Ophiognomonia setacea	CBS 128352	DMW 291.1	BPI 882205	JF514846*	JF319082*	JF514822*	USA	*Quercus palustris*	D.M. Walker
Ophiognomonia setacea	CBS 128354	DMW 310.1	BPI 882208	JF514847*	JF319035*	JF514823*	USA	*Quercus* sp.	D.M. Walker
Ophiognomonia setacea	CBS 131339	DMW 333.2	BPI 882212	JQ414227	JQ414075	JQ414159	Japan	*Quercus acutissima*	D.M. Walker
Ophiognomonia sogonovii	CBS 121914	AR 4000	BPI 872323	EU199190.1*	JQ414055	JQ414139	Russia	*Quercus mongolica*	L. Vasilyeva
Ophiognomonia sogonovii	CBS 131340	DMW 336.3	BPI 882213	JQ414228	JQ414076	JQ414160	Japan	*Quercus mongolica*	D.M. Walker
Ophiognomonia sogonovii	CBS 131341	DMW 337.1	BPI 882214	JQ414229	JQ414077	JQ414161	Japan	*Quercus serrata*	D.M. Walker
Ophiognomonia sogonovii	CBS 131661	DMW 353.1	BPI 882221	JQ414234	JQ414082	JQ414166	Japan	*Quercus mongolica var. grosseserrata*	D.M. Walker
Ophiognomonia trientensis	CBS 131604	DMW 554	BPI 882638	JQ414281	JQ414129	JQ414213	USA	*Alnus* sp.	D.M. Walker
Ophiognomonia tucumanensis	CBS 131364	DMW 549	BPI 882288	JQ414278	JQ414126	JQ414210	Argentina	*Alnus acuminata*	A.Y. Rossman
Ophiognomonia tucumanensis	CBS 131368	LCM 622.01	BPI 879565	JQ414288	JQ414136	JQ414220	Argentina	*Alnus acuminata*	L.C. Mejía
Ophiognomonia vasiljevae	CBS 121253	AR 4298	BPI 877671	EU254977.1*	JQ414060	JQ414144	USA	*Juglans nigra*	M.V. Sogonov
Ophiognomonia vasiljevae	CBS 128353	DMW 303.3	BPI 882206	JF514850*	JF319083*	JF514831*	USA	*Juglans nigra*	M.V. Sogonov
Ophiognomonia vasiljevae	CBS 131436	DMW 550	BPI 882289	JQ414279	JQ414127	JQ414211	USA	*Juglans* sp.	D.M. Walker

AR Dr. Amy Rossman, third author; *BPI* U.S. National Fungus Collections, USDA, ARS, Beltsville, MD; *CBS* Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands; *DMW* Donald M. Walker, first author; *NA* not available; * DNA sequence from an alternative study

Oslo Bioportal (http://www.bioportal.uio.no/) and The Lattice Project (http://boinc.umiacs.umd.edu) web servers were used for performing partitioned ML and Bayesian analyses with the programs GARLI v2.0 (Zwickl 2006) and MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) respectively, with implementation of parameters from Walker et al. (2012). In order to reach convergence, the Bayesian analyses of alignments four and eight were run for 20,000,000 generations.

Phylogenetic species recognition was based on three methods, specifically the genealogical sorting index (*gsi*; Cummings et al. 2008), genealogical concordance phylogenetic species recognition (GCPSR; Talyor et al. 2000), and genealogical nondiscordance (Dettman et al. 2003). The *gsi* is a standardized method to determine exclusive ancestry of predefined groups in a tree. It is based on a 0 to 1 continuum with 0=lack of genealogical divergence from other groups and 1=monophyly. The *gsi* statistic can be used to test hypothesized species lineages measured by coalescent patterns in gene trees against the null hypothesis of no divergence (Cummings et al. 2008). Alignments 5–7 (clades 1–3) were independently tested with *gsi* using 100 trees randomly selected from the GARLI maximum likelihood bootstrap (MLBS) tree distribution with 10,000 permutations to determine statistical significance (P-value$\leq$0.05) using the *gsi* web server (http://www.genealogicalsorting.org/index.php). All 100 *gsi* measurements from the MLBS tree distribution were pooled to calculate an ensemble gsi_T statistic for each marker. The gsi_T statistic is a summary measurement of genealogical exclusivity for a species lineage across the MLBS tree distribution for a given marker. The results from the conditional comparison tests were used for GCPSR and genealogical nondiscordance. Twenty-nine species were evaluated. Since these methods use comparisons of clades consisting of multiple isolates to represent a phylogenetic species, 16 species represented by a single isolate were excluded from the analyses.

Results

Phylogenetic analyses

After manual adjustment and curation in Gblocks, alignment one (ITS) consisted of 410 (73 %) of the original 556 position dataset with 321 constant, 38 non-parsimony informative, and 51 parsimony informative sites; alignment two (*tef-1*α) consisted of 531 (38 %) of the original 1,364 position dataset with 392 constant, 39 non-parsimony informative, and 100 parsimony informative sites; and alignment three (MS204) consisted of 810 (65 %) of the original 1,244 position dataset with 494 constant, 85 non-parsimony informative, and 231 parsimony informative. The combined three-marker alignment consisted of 1,751 of the available 3,164 positions (55 %) with 1,207 constant, 162 non-parsimony informative, and 382 parsimony informative sites. A maximum parsimony (MP) heuristic search of the three marker alignment produced 12 equally parsimonious trees with a length of 1,596 steps (CI=0.490, RI=0.617, RC=0.302, HI=0.510). Only ITS sequences were available for *Ophiognomonia gei* and *O. rubi-idaei.* Therefore these species were not included in the combined alignment but were included in alignment eight. Alignment eight (ITS) consisted of 455 (83 %) of the original 545 position dataset with 385 constant, 17 non-parsimony informative, and 53 parsimony informative sites. A maximum parsimony (MP) heuristic search produced a single most parsimonious tree with a length of 107 steps (CI=0.832, RI=0.933, RC=0.776, HI=0.168). Hereafter, alignments four and eight will be referred to as the "combined alignment" and "ITS alignment" respectively.

Based on the results of the combined alignment, three additional datasets containing taxa corresponding to the three identified major clades were prepared to more fully investigate variation in these clades because many potentially informative sites were discarded due to ambiguous alignment in the all-taxa combined alignment. Alignment five (clade one) consisted of 2,189 (79 %) of the original 2,783 position dataset with 1,684 constant, 125 non-parsimony informative, and 380 parsimony informative sites. A maximum parsimony (MP) heuristic search produced eight equally parsimonious trees with a length of 829 steps (CI=0.765, RI=0.898, RC=0.687, HI=0.235). Alignment six (clade two) consisted of 2,126 (72 %) of the original 2,940 position dataset with 1,617 constant, 85 non-parsimony informative, and 424 parsimony informative sites. A maximum parsimony (MP) heuristic search produced two equally parsimonious trees with a length of 855 steps (CI=0.756, RI=0.879, RC=0.664, HI=0.244). Alignment seven (clade three) consisted of 2,096 (72 %) of the original 2,925 position dataset with 1,538 constant, 166 non-parsimony informative, and 392 parsimony informative sites. A maximum parsimony (MP) heuristic search produced 30 equally parsimonious trees with a length of 1,104 steps (CI=0.655, RI=0.770, RC=0.504, HI=0.345). Hereafter, alignments 5–7 will be referred to as clades one, two, and three, respectively.

The conditional comparison test showed conflict independently between *tef-1*α vs. ITS and MS204 single-marker trees for placement of a single species, *Ophiognomonia lenticulispora*, which was represented by the single isolate CBS 131363. The single-marker alignments were reduced to one isolate representing each species and analyzed to eliminate taxon sampling as a possible reason for any observed incongruence. The same minor conflict remained independently between *tef-1*α vs. ITS and MS204.

Nucleotide substitution models were determined individually for each marker in all eight alignments (Supplementary Table 1). The ML analysis in GARLI v2.0 for the combined analysis resulted in one tree with a -lnL 10931.08 (Fig. 1); clade one resulted in one tree with a -lnL 7963.63 (Fig. 2); clade two resulted in one tree with a -lnL 7605.96 (Fig. 3); clade three resulted in one tree with a -lnL 8916.31 (Fig. 4); alignment of ITS sequences corresponding to clade two resulted in one tree with a -lnL 1888.25 (Fig. 5).

The ML analyses of the combined alignment and clades 1–3 resolves all included species of *Ophiognomonia* (Figs. 1, 2, 3, and 4). Three major clades (100 % PP, ML, MP) were supported. Clade one consists of 15 species that occur on the host families Betulaceae, Fagaceae, and Rosaceae (Fig. 2). Within clade one, a group of closely related species including *O. asiatica, O. kobayashii, O. otanii, O. setacea,* and *O. sogonovii* occur on *Quercus* spp. and *Castanea* spp. within the Fagaceae (100 % PP, 91 % ML, < 70 % MP). Clade two consists of 11 species of *Ophiognomonia* occurring on the host families Juglandaceae, Lauraceae, Rosaceae, and Malvaceae (Fig. 3). One group within clade two (100 % PP, ML, 99 % MP) containing *O. cordicarpa, O. longispora, O. melanostyla,* and *O. sassafras* shares elongated filiform ascospores (Figs. 11, 24, 40, 44), a character not observed among the remaining species of *Ophiognomonia.* Another group (99 % PP, 94 % ML, 86 % MP) within clade two consisting of *O. nipponicae, O. padicola,* and *O. rosae* occurs only on hosts in the Rosaceae. Also within clade two, the species *O. micromegala, O. pseudoclavulata,* and *O. vasiljevae* form a supported group (100 % PP, 99 % ML, 97 % MP) that occurs on hosts in the Juglandaceae, except for *O. lenticulispora,* which was collected on *Prunus* sp. (Fig. 3). Clade three contains 15 species of *Ophiognomonia* on the host families Betulaceae, Juglandaceae, and Salicaceae. One group of eight species is supported (100 % PP, 98 % ML, 92 % MP) within clade three, including *O. alni-viridis, O. bugabensis, O. ibarakiensis, O. intermedia, O. maximowiczianae, O. multirostrata, O. nana,* and *O. tucumanensis,* which occur on *Alnus* spp. and *Betula* spp.

GCPSR and gsi analyses

Twenty-nine of the 45 species of *Ophiognomonia* were tested using the three criteria for GCPSR defined in the methods and were confirmed as distinct evolutionary lineages. The remaining 16 species were represented by a single isolate and could not be subjected to these analyses. Using GCPSR, MS204 supported all 29 species tested (Table 2). Analysis of *tef-1α* resulted in strong support for 27 species, excluding *O. hiawathae* and *O. michiganensis.* Only 18 of 29 species were supported in the ITS gene tree using GCPSR. Genealogical nondiscordance was not observed in any of the 29 species of *Ophiognomonia.* In addition, all species were strongly supported in 2/3 or 3/3 marker genealogies, except for *O. hiawathae* and *O. michiganensis,* which were strongly supported by MS204. The *gsi* results for each marker differed, but were in general agreement with GCPSR of species (Table 2). The gsi_T range of values for MS204 was 0.5727–1.0 with 27 of 29 species≥0.7504. This marker exhibits the highest degree of exclusive ancestry among species for the combination of MLBS trees tested. The gsi_T range of values for *tef-1α* was 0.4782–1.0, with 26 of 29 species≥0.7346 (Table 2). The gsi_T for *O. hiawathae* was not significant indicating incomplete lineage sorting in the *tef-1α* marker for this species. The tree distribution representing the genealogical history of the ITS region indicated high exclusive ancestry for most but not all species of *Ophiognomonia.* The ITS region showed a diverse range of gsi_T values (Table 2; 0.1551–1.0). The *gsi* results for the ITS region were as follows: five species had statistically significant gsi_T<0.5, 21 species with gsi_T> 0.5 and three species with non-statistically significant gsi_T values. ITS sequences representing *Ophiognomonia rubi-idaei* show a high statistically significant gsi_T value (0.8194) suggesting that this species is a distinct evolutionary lineage.

Discussion

Taxonomy

The genus *Ophiognomonia* is a highly diverse group of fungi with economically significant pathogens of shade, lumber, and nut-producing trees (Anderson and LaMadeleine 1978; Behdad 1991; Belisario et al. 2008; Berry 1981; Broders and Boland 2011; Green 2004; Green and Castlebury 2007; Juhasova et al. 2006; Neely and Black 1976; Pennycook 2007; Salahi et al. 2009). In this study, descriptions and illustrations for 27 new combinations and species and 12 previously recognized species are provided as well as a key to all species of *Ophiognomonia*.

Monod (1983) characterized the genus *Ophiognomonia* as having elongated filiform ascospores with 1–3 septations. Of the eight species recognized by Monod (1983) in *Ophiognomonia, O. padicola,* and *O. sassafras* are confirmed in this genus with molecular data by Sogonov et al. (2008). Many of the species recognized here as members of *Ophiognomonia* were placed in the genus *Gnomonia* by Monod (1983). He characterized species in the genus *Gnomonia* as having asci with 8, rarely 2, 4, or 20–30, ascospores each with a median to slightly submedian septum and appendages. Although included in the genus

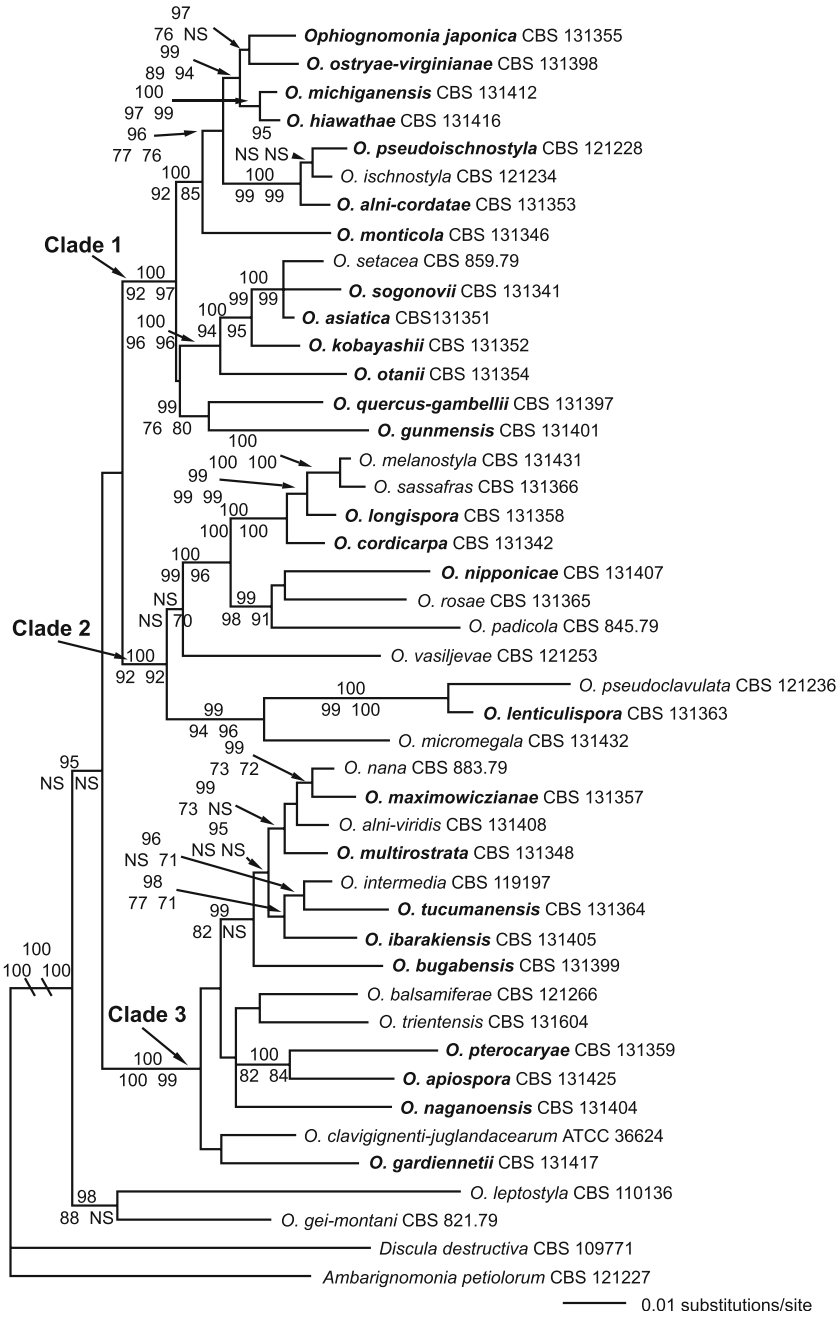

Fig. 1 ML phylogenetic analysis (ML score=-lnL 10931.08) of ITS, MS204, and *tef-1α* sequences of 43 species in *Ophiognomonia* and two outgroup taxa within the Gnomoniaceae. Bayesian posterior probabilities≥95 % are displayed above each branch. GARLI ML bootstrap values ≥70 % are displayed to the bottom left and MP bootstrap values≥70 % to the bottom right of each branch. Taxa in bold are new combinations or new species

Gnomonia by Monod (1983), the following species were accepted by Sogonov et al. (2008) and confirmed herein as members of the genus *Ophiognomonia: O. alni-viridis, O. gei-montani, O. intermedia, O. leptostyla, O. rosae, O. rubi-idaei, O. setacea,* and *O. trientensis.* In addition *O. micromegala* was placed in the genus *Plagiostoma* based on the presence of lateral perithecial necks and *O. nana* in the genus *Gnomoniella* based on aseptate ascospores by Monod (1983). A culture (BRIP 29308a) of *O. elasticae* (Koords.) M. Monod was obtained, sequenced, and determined to fall outside of the Gnomoniaceae, in the Basidiomycota. The remaining species of *Ophiognomonia* recognized by Monod (1983), specifically *O. capillaris, O. langii,* and *O. lapponica,* could not be obtained for this study. Barr's (1978) generic concepts of *Gnomonia, Gnomoniella, Ophiognomonia,* and *Plagiostoma* were accepted by Monod (1983), however, the species in each genus differ. She recognized only the type species of *Ophiognomonia*, *O. melanostyla*.

Within the genus *Ophiognomonia* most morphological characters such as shape and size of perithecia and perithecial necks and ascospore length, width, and septation have limited use for identification of species of *Ophiognomonia.* The most common morphological characteristic in *Ophiognomonia* occurring in 28 of 45 species is fusiform ascospores that are approximately 10–20×2–4 μm with a

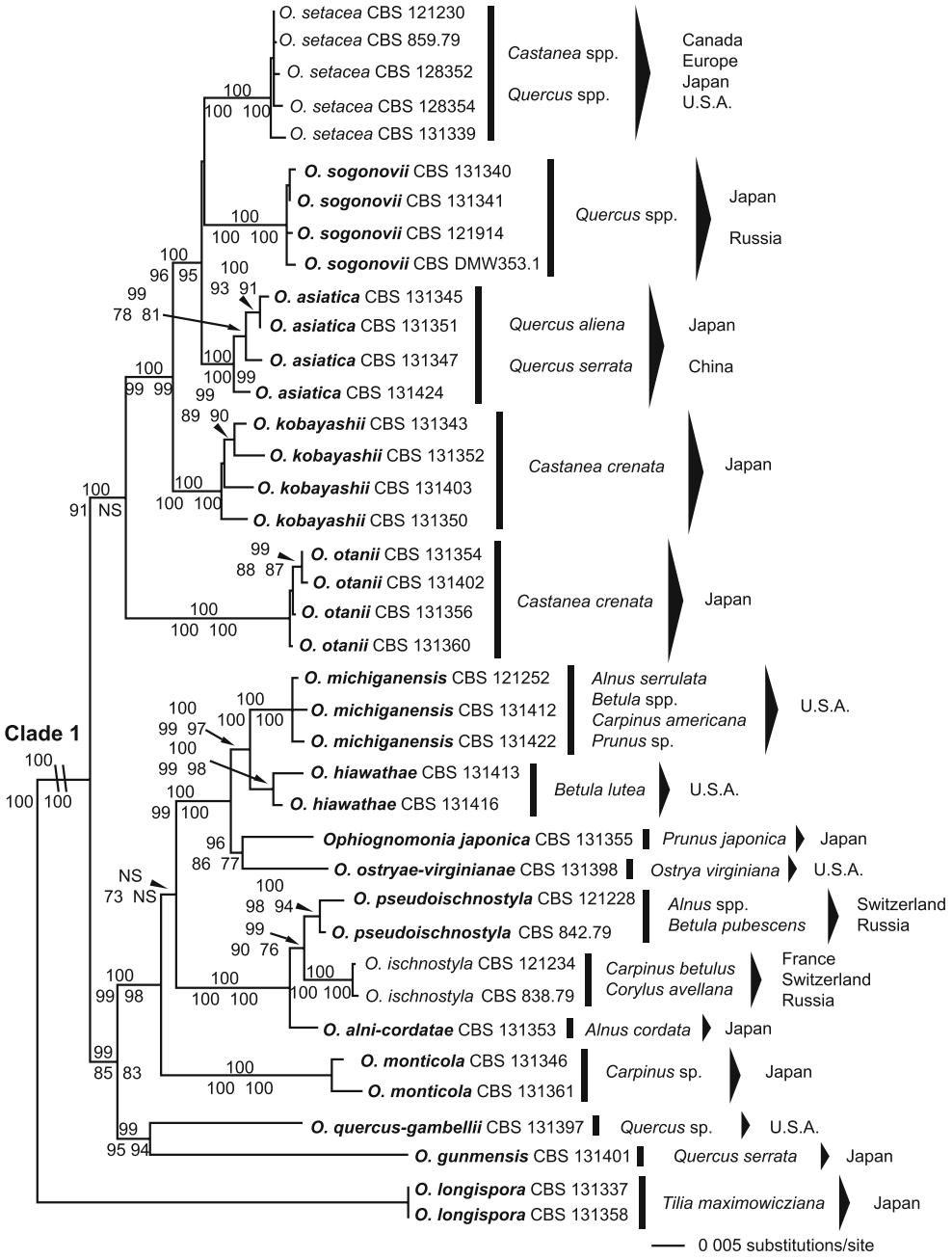

Fig. 2 ML phylogenetic analysis (ML score=-lnL 7963.63) of ITS, MS204, and *tef-1α* sequences of 15 species in *Ophiognomonia* (Clade one) and one outgroup taxon within *Ophiognomonia*. Bayesian posterior probabilities≥95 % are displayed above each branch. GARLI ML bootstrap values ≥70 % are displayed to the bottom left and MP bootstrap values≥70 % are displayed to the bottom right of each branch. Taxa in bold are new combinations or new species

median septum. A distinct submedian septum was observed in ascospores of *O. alni-cordatae, O. apiospora, O. geimontani,* and *O. otanii* (Figs. 6, 8, 14, 35). Aseptate ascospores were documented only in *O. nana* (Fig. 32). *Ophiognomonia cordicarpa, O. longispora, O. melanostyla,* and *O. sassafras* forming a phylogenetically distinct group were the only species with filiform ascospores (Figs. 11, 24, 26, 42). Ascospore appendages were observed in *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.* Uncommonly large ascospores (40×7 μm) for *Ophiognomonia* were observed in *O. micromegala* (Fig. 28). Among the species of *Ophiognomonia,* only *O. lenticulispora* and *O. pseudoclavulata* have oval to ellipsoidal ascospores (Fig. 22, 36). Multiple-necked perithecia were occasionally observed in *O. michiganensis* and *O. multirostrata,* a phenomenon often occurring in culture, but rarely in nature for species of *Gnomoniopsis* and *Ophiognomonia* (Fig. 27, 30; Sogonov et al. 2008; Walker et al. 2010). *Ophiognomonia apiospora* has an unusually thick perithecial cell wall for this genus that becomes distinctly concave upon drying (Fig. 8). No single, distinct, morphological characteristic allows recognition of individual species in the phylogenetically diverse genus *Ophiognomonia.*

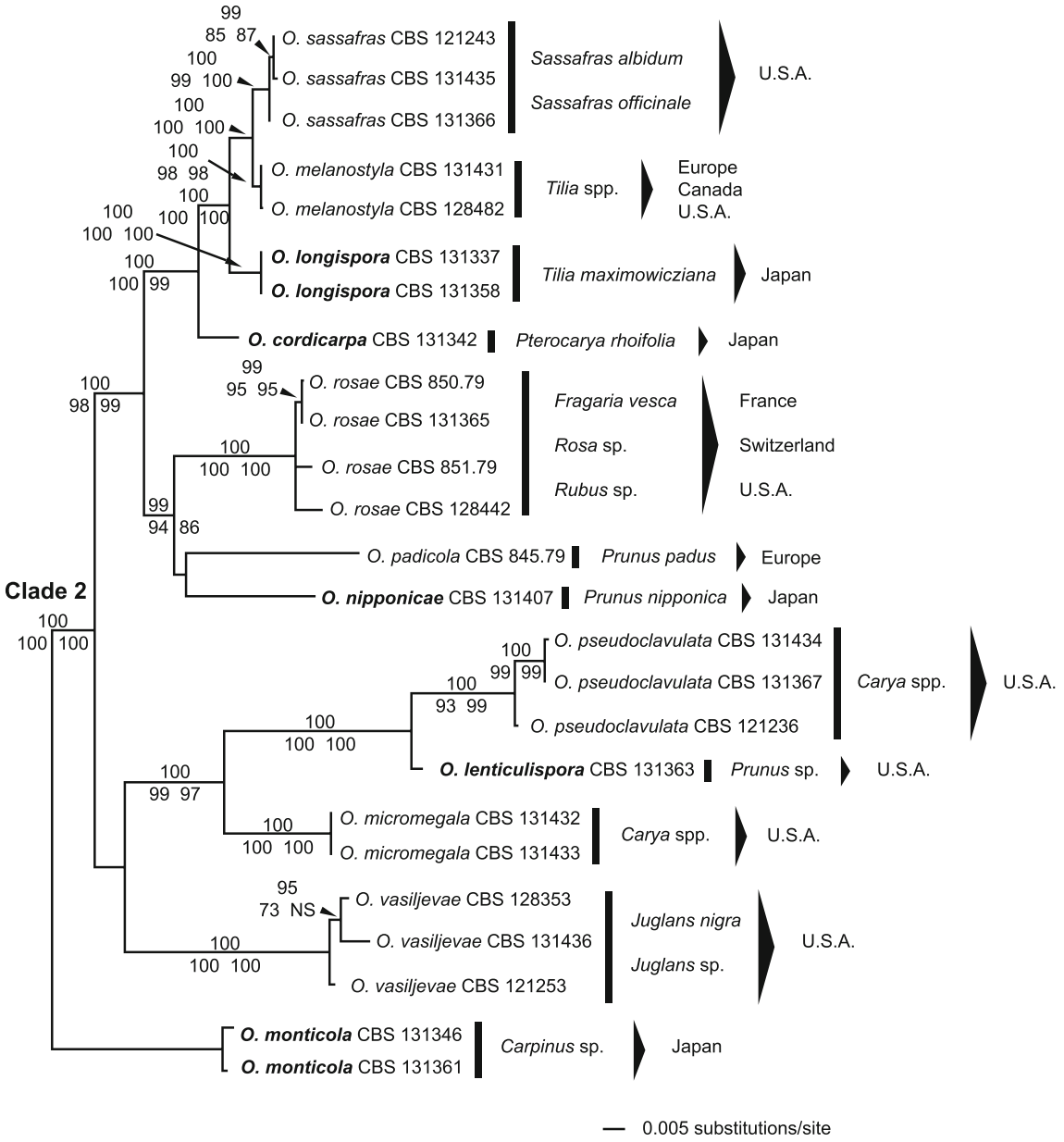

Fig. 3 ML phylogenetic analysis (ML score=-lnL 7605.96) of ITS, MS204, and *tef-1α* sequences of 11 species in *Ophiognomonia* (Clade two) and one outgroup taxon all within *Ophiognomonia*. Bayesian posterior probabilities≥95 % are displayed above each branch. GARLI ML bootstrap values ≥70 % are displayed to the bottom left and MP bootstrap values≥70 % are displayed to the bottom right of each branch. Taxa in bold are new combinations or new species

Geographic distribution

Barr (1978) documented the North American distribution of gnomoniaceous species as far north as British Columbia, Canada. The northernmost range of *Ophiognomonia* is expanded here to Finland where *O. rosae* was collected; the southernmost distribution is extended to Central America (Panama) where *O. bugabensis* was collected and to South America (Argentina) for *O. tucumanensis*. Sogonov et al. (2008) documented several genera in the Gnomoniaceae including *Ophiognomonia* occurring in Russia. Mejía et al. (2011a) expanded the biogeographic range of the Gnomoniaceae by describing the monotypic genus *Occultocarpon* and several new species of *Plagiostoma* from the Yunnan province of China. This study presents the first report of the genus *Ophiognomonia* from China. Kobayashi (1970) documented a single species of *Ophiognomonia, O. setacea,* in Japan, and that report is confirmed here. On a two-week trip to Japan, 16 new species were collected and are described here. These results suggest that gnomoniaceous fungi are plentiful throughout temperate regions.

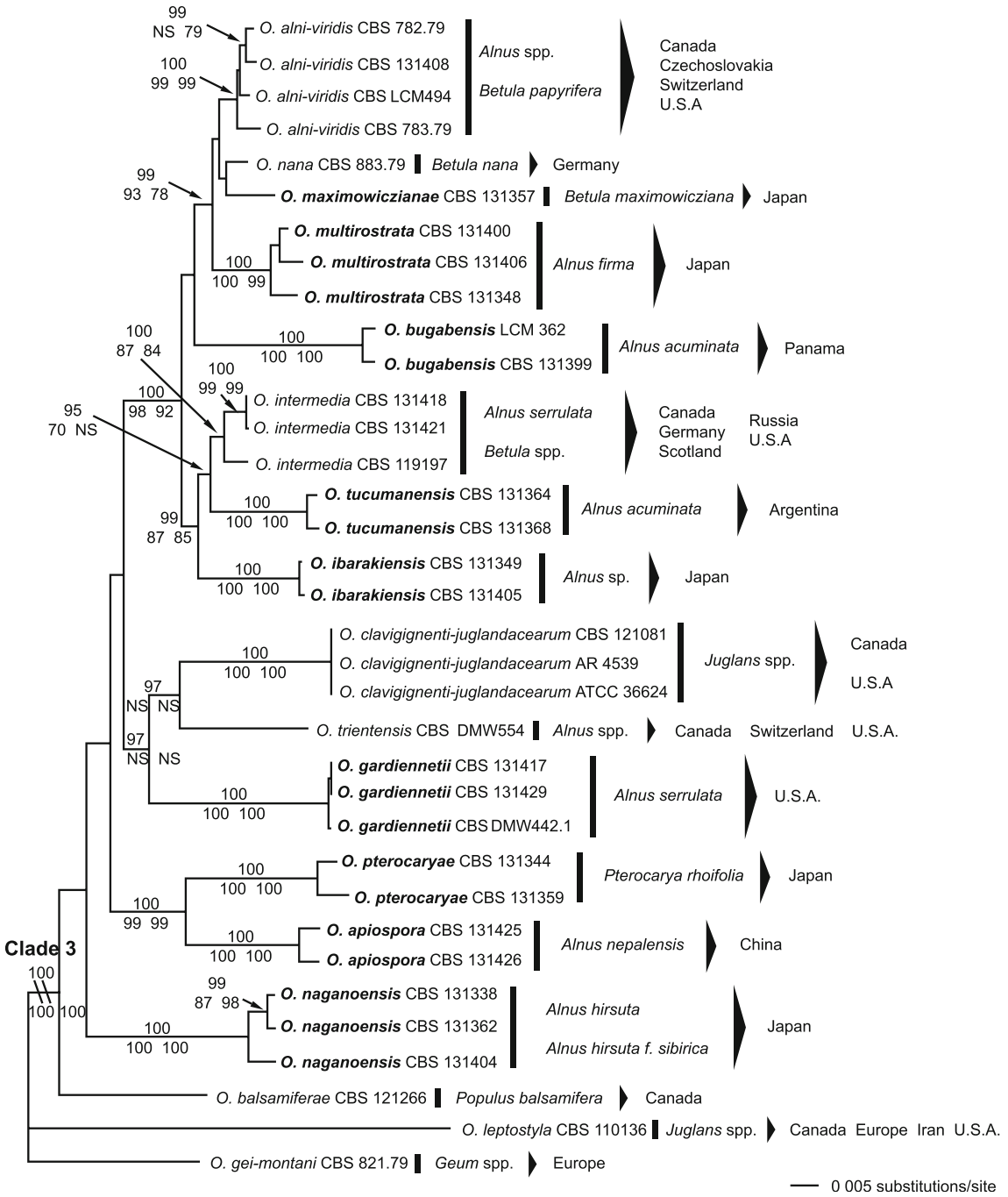

Fig. 4 ML phylogenetic analysis (ML score=-lnL 8916.31) of ITS, MS204, and *tef-1*α sequences of 15 species in *Ophiognomonia* (Clade three) and two outgroup taxa all within *Ophiognomonia*. Bayesian posterior probabilities≥95 % are displayed above each branch. GARLI ML bootstrap values ≥70 % are displayed to the bottom left and MP bootstrap values≥70 % are displayed to the bottom right of each branch. Taxa in bold are new combinations or new species

The biogeographic structure represented in the phylogeny of *Ophiognomonia* indicates allopatric speciation as a driving force for several endemic species in this group. Multiple species have limited geographic distribution to regions such as Japan/China, Europe/North America, or Central/South America. *Ophiognomonia setacea* is the only exception, exhibiting a global distribution without geographic constraints. For example, 14 species are endemic in Japan, two in Central and South America, 13 in North America, and four in Europe suggesting that these species are genetically and, in many cases, geographically isolated from other species of *Ophiognomonia.* It is unclear to what extent these taxa are truly endemic or are present but undocumented in other locations.

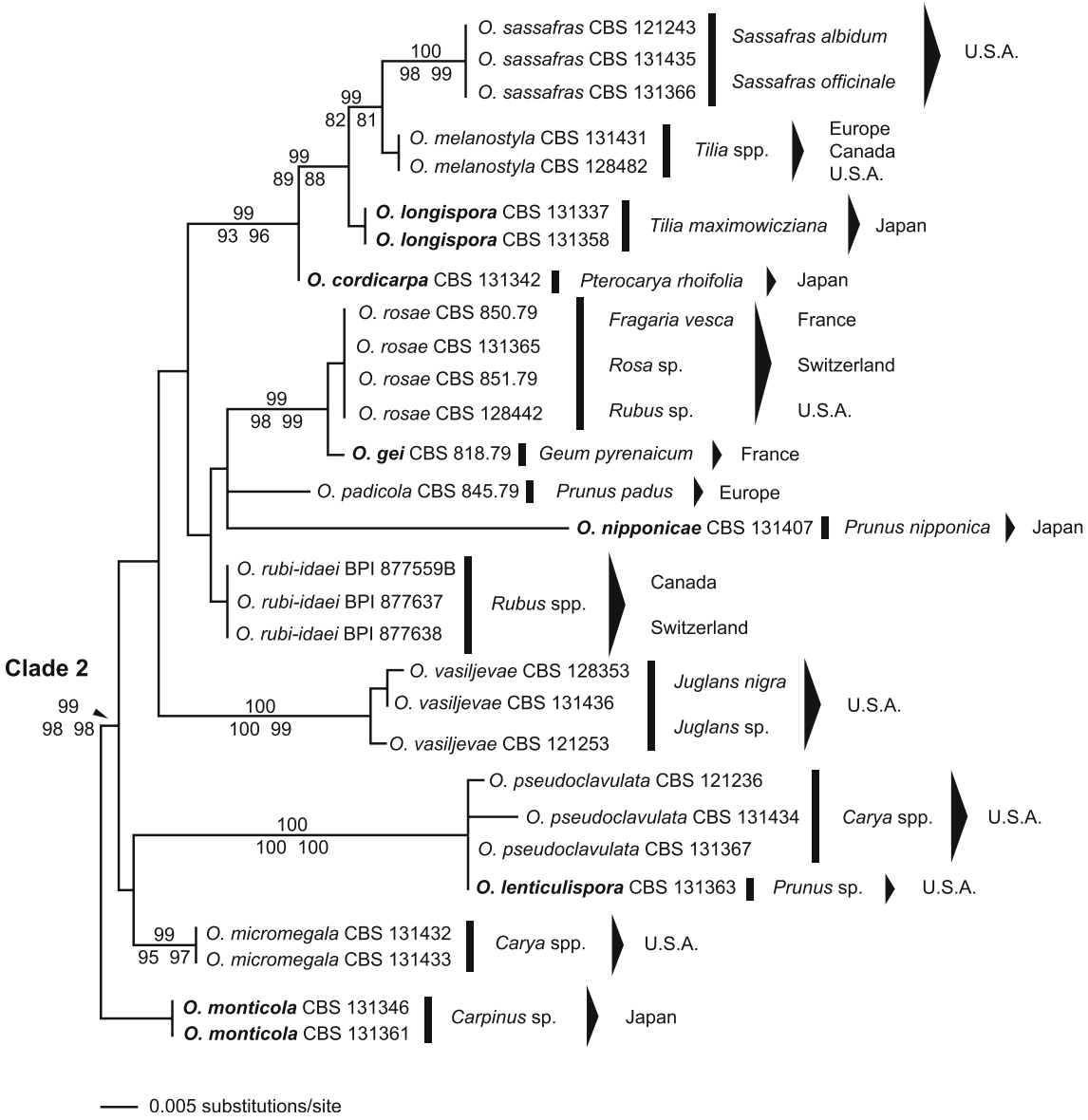

Fig. 5 ML phylogenetic analysis (ML score=-lnL 1888.25) of ITS sequences of 11 species in *Ophiognomonia* (Clade two) and one outgroup taxon all within *Ophiognomonia*. Bayesian posterior probabilities≥95 % are displayed above each branch. GARLI ML bootstrap values ≥70 % are displayed to the bottom left and MP bootstrap values≥70 % are displayed to the bottom right of each branch. Taxa in bold are new combinations or new species

Host associations

Phylogenetic analyses of variable molecular markers are the primary means of species delimitation in *Ophiognomonia*. This genus has a diverse host range occurring on plants in the families Betulaceae, Fagaceae, Juglandaceae, Lauraceae, Malvaceae, Platanaceae, Rosaceae, Salicaceae, and Sapindaceae. Most species of *Ophiognomonia* show preference to a single host genus or several genera from the same host family. For example, *O. monticola* was collected on *Carpinus* sp. (Betulaceae) from Japan and *O. rosae* on *Fragaria vesca, Rosa* sp., and *Rubus* sp. (Rosaceae) from Europe and the U.S. However, one species, *O. michiganensis,* was associated with genera in the Betulaceae and Rosaceae similar to host/fungus associations for *Apiognomonia errabunda,* which causes anthracnose disease of shade trees in 10 different plant families (Sogonov et al. 2007). The genus *Alnus* is the most common host plant for species of *Ophiognomonia.* Thirteen species in clades one and three (Figs. 2, 4) are associated with *Alnus* spp. *Ophiognomonia balsamiferae* on *Populus* spp. is the only species of *Ophiognomonia* that occurs on the Salicaceae and thus may represent a host jump to a novel host family. Despite extensive collecting on salicaceous hosts, no additional species of

Table 2 Phylogenetic species recognition

Clade #	Species	Genealogical sorting index GSI				GCPSR			
		ITS *gsiT*	MS204 *gsiT*	*tef-1a gsiT*	Combined *gsiT*	ITS n = ≥ 70%	MS204 n = ≥ 70%	*tef-1a* n = ≥ 70%	Combined n = ≥ 70%
1	*O. setacea*	0.8835*	1.0*	0.9911*	1.0*	NS	x	x	x
	O. sogonovii	0.9338*	0.9972*	0.9972*	1.0*	x	x	x	x
	O. asiatica	0.4692*	0.9972*	0.9848*	1.0*	NS	x	x	x
	O. kobayashii	0.3853*	0.9837*	1.0*	0.9972*	NS	x	x	x
	O. otanii	0.9237*	0.9945*	1.0*	0.9918*	x	x	x	x
	O. michiganensis	0.2717*	1.0*	0.6815*	1.0*	NS	x	NS	x
	O. hiawathae	0.1321	1.0*	0.2174	1.0*	NS	x	NS	x
	O. pseudoischnostyla	0.1411	1.0*	0.7346*	1.0*	NS	x	x	x
	O. ischnostyla	0.1207	1.0*	1.0*	1.0*	NS	x	x	x
	O. monticola	0.917*	1.0*	1.0*	1.0*	x	x	x	x
2	*O. sassafras*	0.9934*	0.5727*	1.0*	0.9963*	x	x	x	x
	O. melanostyla	0.8323*	0.7504*	0.9191*	0.9739*	x	x	x	x
	O. longispora	0.9547*	0.9895*	0.9226*	1.0*	x	x	x	x
	O. rosae	1.0*	1.0*	0.9914*	0.9942*	x	x	x	x
	O. pseudoclavulata	0.6309*	0.640*	1.0*	1.0*	x	x	x	x
	O. micromegala	0.9321*	1.0*	0.4782*	0.9947*	x	x	x	x
	O. vasiljevae	0.9927*	0.9963*	0.9818*	1.0*	x	x	x	x
	O. rubi-idaei	0.8194*	NA	NA	NA	x	NA	NA	NA
3	*O. alni-viridis*	0.2083*	0.9846*	0.9890*	0.9972*	NS	x	x	x
	O. multirostrata	0.6435*	0.9893*	0.9893*	0.9858*	NS	x	x	x
	O. bugabensis	0.8609*	0.9845*	0.9742*	0.9793*	x	x	x	x
	O. intermedia	0.1551*	0.8186*	0.9415*	0.9858*	NS	x	x	x
	O. tucumanensis	0.6406*	0.9948*	1.0*	1.0*	NS	x	x	x
	O. ibarakiensis	0.8449*	0.9896*	0.9948*	1.0*	x	x	x	x
	O clavigignenti-juglandacearum	0.9079*	1.0*	1.0*	1.0*	x	x	x	x
	O. gardiennetii	0.9929*	1.0*	1.0*	0.9964*	x	x	x	x
	O. pterocaryae	0.9244*	1.0*	1.0*	1.0*	x	x	x	x
	O. apiospora	0.9587*	0.9948*	0.9845*	0.9948*	x	x	x	x
	O naganoensis	0.9858*	0.9964*	1.0*	0.9964*	x	x	x	x

The Clade # correlates with Figs. 2, 3, and 4; The GSI statistic is based on a 0 to 1 continuum, with 0 = lack of genealogical divergence from other groups and 1 = monophyly; * = statistical significant P-value ≤ 0.05; x = parsimony bootstrap support ≥ 70%; NS = parsimony bootstrap support < 70%

Ophiognomonia were discovered in this family. Multiple species including *O. clavigignenti-juglandacearum, O. leptostyla, O. micromegala, O. pseudoclavulata,* and *O. vasiljevae* occur on plants in the Juglandaceae in addition to *O. cordicarpa* and *O. pterocaryae,* the first records of the Gnomoniaceae on the host genus *Pterocarya* in the Juglandaceae. Several patterns of host plant association at the family rank were observed throughout the phylogeny of *Ophiognomonia*. A group of closely related species including *O. asiatica, O. kobayashii, O. otanii,* and *O. sogonovii* are specific to *Quercus* spp. and *Castanea* spp. within the Fagaceae (Fig. 2). In addition, a group including *O. nipponicae, O. padicola,* and *O. rosae* occur only on hosts in the Rosaceae (Fig. 3). Similarly a distribution of fungal species on only one host family was observed for other genera in the Gnomoniaceae. Mejía et al. (2011c) discovered 11 species of *Plagiostoma* associated with the Salicaceae while Walker et al. (2010) found similar host/fungus relationships in the genus *Gnomoniopsis*. Sogonov et al. (2008) observed similar relationships for species of *Gnomonia* associating with a single host genus or species within the Coryloideae. A clade consisting of eight species of *Ophiognomonia,* including *O. alni-viridis, O. bugabensis, O. ibarakiensis, O. intermedia, O. maximowiczianae, O. multirostrata, O. nana,* and *O. tucumanensis* are host specific to *Alnus* spp. and *Betula* spp. (Fig. 4). The genus *Cryptosporella* exhibits similar host/fungus

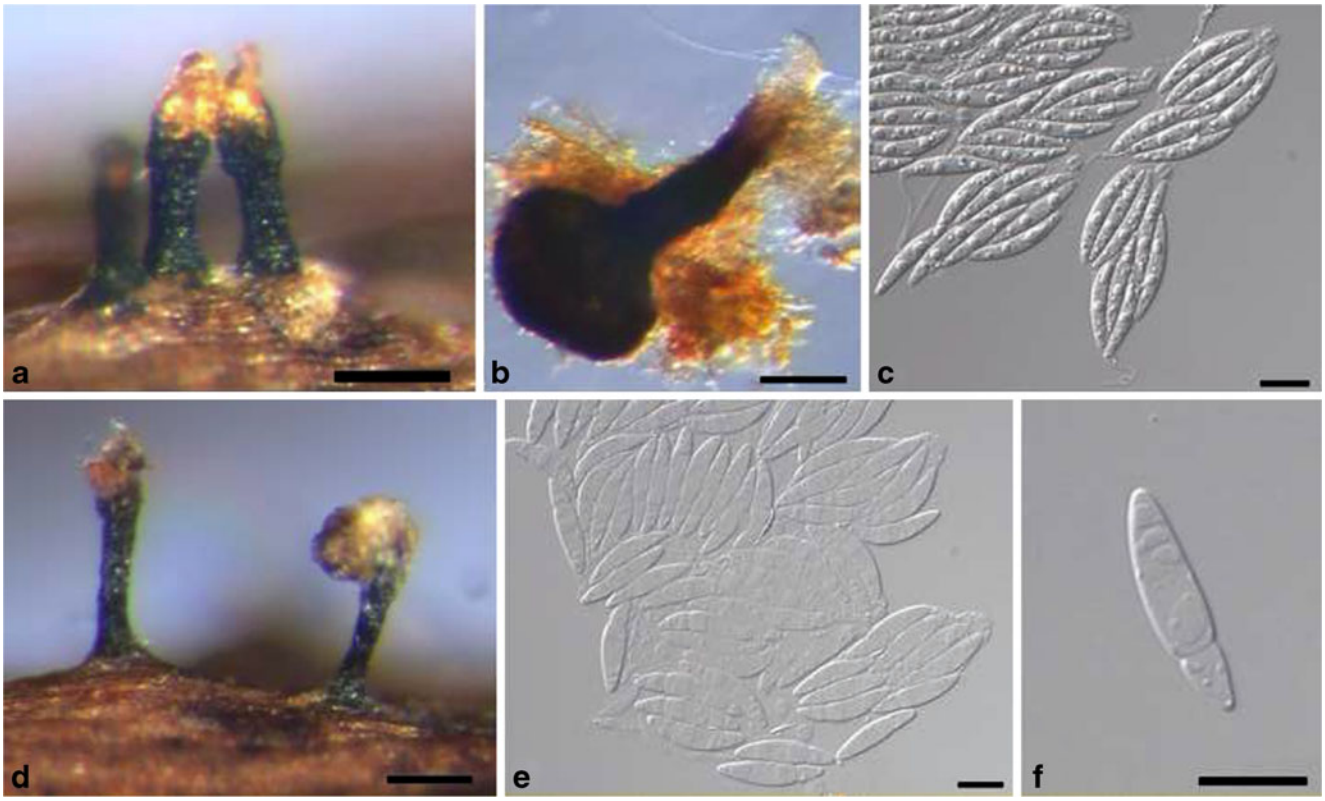

Fig. 6 *Ophiognomonia alni-cordatae.* **a**–**f**. Holotype BPI 882233. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

associations on *Alnus*/*Betula* (Mejía et al. 2008, 2011b). These examples suggest close host/fungus associations and possible host specificity or coevolution within the Gnomoniaceae.

Phylogeny of *Ophiognomonia*

The criteria used here for GCPSR proved useful for species recognition in the Gnomoniaceae. Similar criteria for GCPSR have been used in the model organisms *Aspergillus* spp. (Pringle et al. 2005), *Neurospora* (Dettman et al. 2003), and *Fusarium* spp. (O'Donnell et al. 2004; Sarver et al. 2011). For example, in Pringle et al. (2005) a distinct evolutionary lineage was recognized if the majority of single-marker genealogies were congruent. Two criteria were considered important for GCPSR in Dettman et al. (2003). A clade must be present in (1) the majority of single-marker genealogies or (2) strongly supported with a single-marker and lack genealogical nondiscordance in any other locus genealogy. These GCPSR concepts were expanded here by including the genealogical sorting index (*gsi*) to determine exclusive genetic ancestry (Cummings et al. 2008).

The *gsi* provided a tree-based measure for identification of reciprocally monophyletic species clades (Cummings et al. 2008). For example, the genealogies constructed for *O. multirostrata, O. setacea,* and *O. tucumanensis* using ITS, lack support under GCPSR. However, *gsi* of the ITS tree distribution indicate near exclusive ancestry (Table 2; gsi_T= 0.6435*/0.8835*/0.6406* respectively). The *gsi* measure can also be used to confirm and quantify the lack of genealogical structure indicated by GCPSR for a species clade at a given locus. For example, in the ITS region, *O. alni-viridis, O. asiatica, O. kobayashii,* and *O. intermedia* are not supported under GCPSR, which is confirmed and quantified by low gsi_T values (Table 2). An explanation for the previously mentioned example is that time to evolve reciprocal monophyly is longer than time since initial genetic isolation (Tajima 1983; Hudson and Coyne 2002; Rosenberg and Harrison 2003). *Ophiognomonia hiawathae* and *O. michiganensis* were the least supported species in single-marker genealogies under the GCSPSR criteria used here (Table 2). However, both the gsi_T and GCPSR analyses for the combined dataset detected distinct genealogical structure for these species. Cummings et al. (2008) observed similar results using the gsi_T statistic to evaluate single-marker genealogies of field crickets (*Grylllus* spp.; dataset from Broughton and Harrison 2003). When analyzing the combined marker dataset for field crickets, genealogical structure at the species level became apparent (Cummings et al. 2008).

Resolving various taxonomic ranks of phylogenetic relationships requires markers with signal at different levels of divergence or different rates of evolution (Hillis and Dixon

1991; Townsend 2007). The markers ITS, MS204, and *tef-1α* were selected for this study based on evidence from Walker et al. (2012), which assessed various combinations of five markers using phylogenetic informativeness tests (Townsend 2007) and determined this combination of three markers to fully recover the five-marker topology with equivalent or higher support for branches. The markers MS204 and *tef-1α* performed exceptionally well in nearly all cases under the criteria for GCPSR (Table 2). The ITS region (ITS1, 5.8 S rDNA and ITS2) performed poorly, most likely due to the low rate of evolution in this marker (Walker et al. 2012).

Three clade-specific alignments (Figs. 2, 3, and 4) were necessary to make accurate decisions of homologous intron regions in ITS, MS204, and *tef-1α*. Exclusion of unnecessary positions after alignment across the entire genus caused a great loss of phylogenetic signal and did not support the true molecular diversity in each species clade. In addition, hidden phylogenetic signal in single-marker analyses often becomes apparent in concatenated analyses (Sullivan 1996). Several species not supported in individual marker analyses were strongly supported by the combined three-marker analysis under the criteria proposed here for GCPSR (Table 2). Similar results were indicated by Wild and Maddison (2008), who determined the necessity of multiple-marker concatenation for reconstructing the beetle tree of life.

Conclusion

This study is an account of the 45 currently known species of *Ophiognomonia* including 25 species new to science. Developing phylogenetic concepts for species recognition in an economically significant group of fungi that lack distinct morphological characters provide the basis for future studies of Gnomoniaceae and other non-model organisms. Knowledge of the species of *Ophiognomonia* has interesting ecological implications given their association and pathogenic potential on important shade, lumber, and nut-producing trees. Accurate species definition is essential for developing effective measures and quarantine policies to control the diseases they cause and spread of these plant pathogens. Additional collection of this highly diverse group will likely lead to the discovery of many new species in diverse habitats worldwide and associations with known and novel host plants.

Taxonomy

Ophiognomonia (Sacc.) Sacc., Syll. Fung. 14: 613. 1899. Lectotype designated by Höhnel (1919): *Ophiognomonia melanostyla* (DC.: Fr.) Berl.

≡ *Gnomoniella* subgenus *Ophiognomonia* Sacc., Syll. Fung. 1: 419. 1882.

Perithecia solitary, aggregated up to three, or in loose clusters, without stroma, epiphyllous and hypophyllous on overwintered leaf blades or on overwintered petioles, rachises, stems, or fruits of woody or herbaceous plants. Perithecia dark brown to glossy black, rarely cream, globose to subglobose, immersed or partially erumpent, occasionally causing host tissue to swell and break. Neck central, lateral, or marginal, straight, curved, or sinuous, long to short. Asci fusiform to oval or filiform, apical ring often conspicuous, eight ascospores per ascus arranged uni-, bi-, and multiseriate or parallel, occasionally intertwined. Ascospores two-celled, rarely one-celled, oval, fusiform, or filiform, ends blunt to rounded, with or without appendages.

Hosts: On Betulaceae, Fagaceae, Juglandaceae, Lauraceae, Malvaceae, Platanaceae, Rosaceae, Salicaceae, and Sapindaceae.

Ophiognomonia alni-cordatae D.M. Walker, sp. nov. Figure 6a–f.

MycoBank: MB 564079

Etymology: alni-cordatae refers to the host on which the holotype was collected.

Holotypus: JAPAN, NAGANO: Ueda-shi, Sugadaira, Kakuma River Trail, on overwintered leaves of *Alnus cordata,* 14 April 2010, D.M. Walker (BPI 882233, culture DMW 384.1=CBS 131353).

Perithecia immersed, occasionally causing host tissue to swell, on leaf petioles and veins, epiphyllous or hypophyllous, solitary or aggregated up to two, glossy black, globose to subglobose, (134–)177–234 μm high×228–294 μm diam (mean=182×261, S.D. 49.7, 46.7, n1=3, n2=2). Necks central to marginal, mostly straight or curved to sinuous, occasionally swollen at tip, (180–)189–394(–438) μm long (mean=263, S.D. 69.8, *n*=18). Asci fusiform with rounded or papillate apex and acute or long tapering stipe, apical ring conspicuous, (43–)45–50(–52)×(13–)16–21(–22) μm (mean=48×18, S.D. 3.6, 2.6, n1=8, n2=11), with ascospores arranged irregularly uni- to multiseriate. Ascospores fusiform, ends rounded, straight to slightly curved, one-septate, distinct submedian septum, slight constriction at septum, (21–)22–24(–25)×(4–)5–6(–7) μm (mean=22.6×5.5, S.D. 1.2, 0.7, n1=27, n2=25).

Habitat: On dead leaves of *Alnus cordata* (Loisel.) Duby (Betulaceae).

Distribution: Japan (Nagano prefecture).

Notes: Ophiognomonia alni-cordatae is one of 17 species known from Japan, and one of four occuring on *Alnus* from this country. A distinct submedian septum was only observed in ascospores of four species including, *O. alni-cordatae, O. apiospora, O. gei-montani,* and *O. otanii.*

Ophiognomonia alni-viridis (Podlahova & Svrček) Sogonov, Stud. Mycol. 62: 55. 2008. Figure 7a–j.

Basionym: *Gnomonia alni-viridis* Podlahova & Svrček, Česká Mycol. 24: 129. 1970.

MycoBank: MB 512215

Perithecia immersed, occasionally causing host tissue to swell, on leaf blades, veins, and petioles, hypophyllous and epiphyllous, solitary or aggregated up to two, glossy

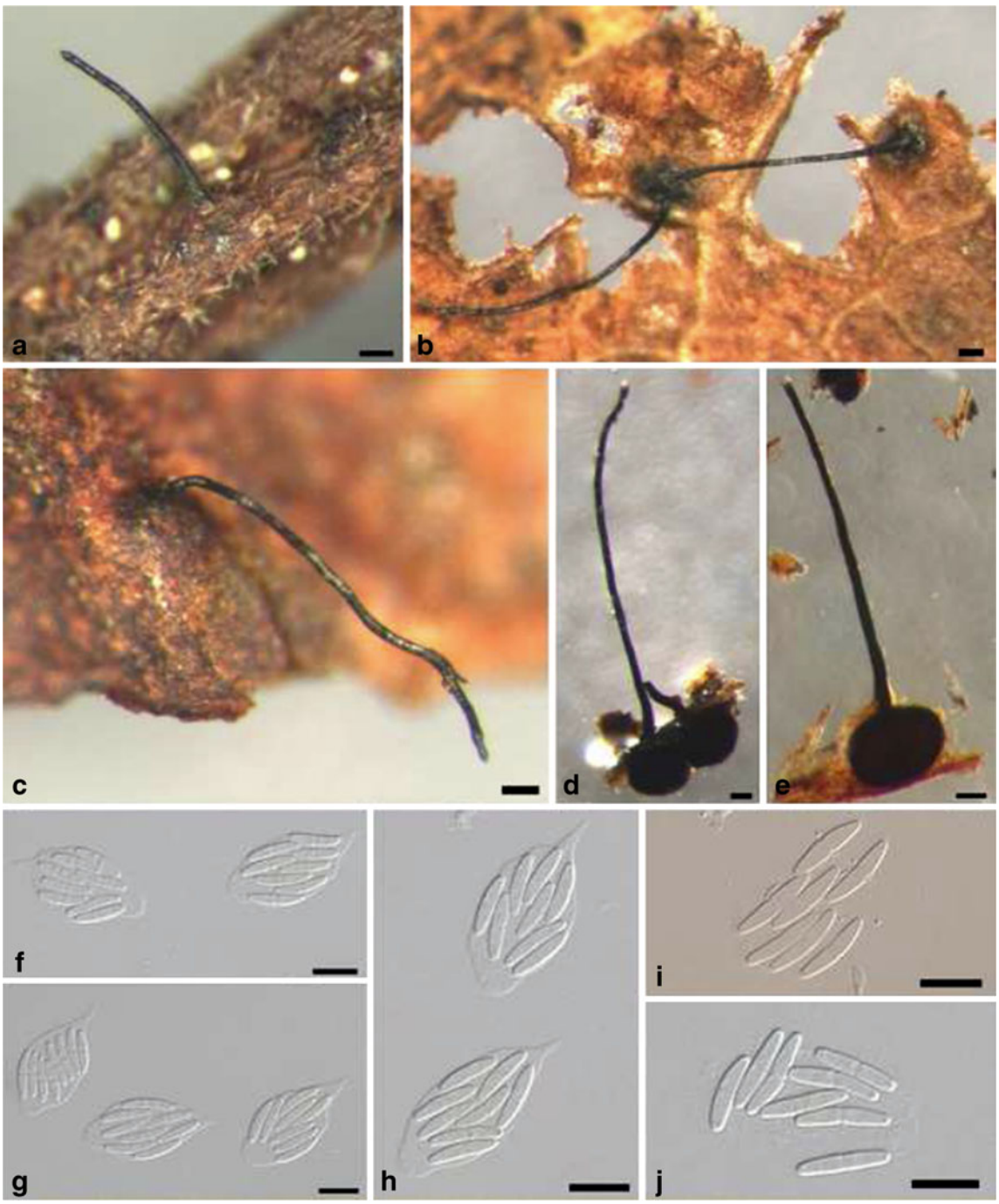

Fig. 7 *Opiognomonia alni-viridis*. **a**, **e**, **i**. BPI 879541; **b**–**d**, **f**–**h**, **j**. BPI 879541. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

black, subglobose, (135–)136–301(–311) μm high×(187–)197–363(–432) μm diam (mean=235×296, S.D. 59.5, 65.6, n1=15, n2=15). Necks central, straight, curved, or slightly sinuous, (331–)641–1,620(–1,653) μm long (mean=1,069, S.D. 371.1, *n*=20). Asci ellipsoid to fusiform with papillate or rounded apex, stipe acute or long tapering, apical ring conspicuous, (28–)29–43(–50)×(8–)9–18(–19) μm (mean=34×15, S.D. 4.6, 2.5, n1=30, n2=28), ascospores arranged parallel or irregularly uniseriate to multiseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, slightly constricted at septum, each cell with 0–2 distinct and several small guttules, (11–)12–16(–17)×2–3 μm (mean=14×3, S.D. 1.6, 0.5, n1=30, n2=30).

Habitat: On overwintered leaves of *Alnus rhombifolia* Nutt., *A. serrulata* (Aiton) Willd., *A. sinuata* Rydb., *A. viridis* (Chaix) D.C., *Betula papyrifera* Marshall, and overwintered fruits of *A. viridis* (Betulaceae).

Distribution: Canada (British Columbia), Europe (Czech Republic, Switzerland), and United States (CA, MI, NY, WA).

Materials examined: CANADA, BRITISH COLUMBIA: 15 km south of Princeton, near Indian Reserve #3, on overwintered leaves of *Betula papyrifera,* 13 May 2006, M.V. Sogonov (BPI 877600, GenBank EU 254869); CZECH REPUBLIC: on overwintered fruits of *Alnus viridis,* 14 July 1969, coll. R. Podlahová, det. Svrček (PRM 685743, HOLOTYPE of *Gnomonia alni-viridis,* PRM); SWITZERLAND: Valais, vicinity of Martigny, on overwintered leaves of *Alnus viridis,* 21 May 2005, M. Monod (BPI 877585A, GenBank EU 254866). UNITED STATES, CALIFORNIA: Shasta County, Shasta, Trinity National Park, Ellery Creek, on *Alnus rhombifolia,* 19 May 2008, L.C. Mejía, det. D.M. Walker (BPI 879529, culture LCM 459.01); MICHIGAN: Houghton County, boat dock near FJ McClain Campground, on overwintered leaves of *Betula* sp., 31 May 2010, D.M. Walker (BPI 882251, culture DMW 439.3=CBS 131408); NEW YORK: Franklin County, Adirondack high peaks region, Adirondack Loj, trail head, on overwintered leaves of *Betula papyrifera,* 9 June 2007, L.C. Mejía, det. D.M. Walker (BPI 881497, cultures LCM 158.01, LCM 158.02); NEW YORK: White Face Mountain, 4,000 ft elevation, on *Alnus serrulata,* 12 June 2007, L.C. Mejía, det. D.M. Walker (BPI 881512, cultures LCM 164.01, LCM 164.02); WASHINGTON: King County, Mount Baker-Snoqualmie National Forest, Snoqualmie ranger district, near exit 42 on highway US 90, on overwintered leaves of *Alnus viridis,* 16 May 2006, M.V. Sogonov (BPI 877595, GenBank EU 254867); WASHINGTON: Clallam County, Olympic National Park, Heart O' the Hills Campground, on *Alnus sinuata,* May 2008, L.C. Mejía, det. D.M. Walker (BPI 879541, culture LCM 494=CBS 128358).

Notes: Ophiognomonia alni-viridis is one of four species that occur on both *Alnus* spp. and *Betula* spp. in the Betulaceae. This species has relatively long perithecial necks compared to many other species in *Ophiognomonia.*

Ophiognomonia apiospora L.C. Mejía & D.M. Walker, sp. nov. Figure 8a–g.

MycoBank: MB 564080

Etymology: apiospora refers to the distinct submedian location of the ascospore septum.

Holotypus: CHINA, YUNNAN PROVINCE: Kunming, Kunming Institute of Botany, botanical garden, on overwintered leaves of *Alnus nepalensis,* 12 July 2008, L.C. Mejía, det. D.M. Walker (BPI 879601, ex-type cultures LCM 503.05=CBS 131425, LCM 503.06=CBS 131426).

Perithecia immersed, occasionally causing host tissue to swell, concave from base when dry, thick cell walls, on leaf petioles and veins, hypophyllous and epiphyllous, solitary or aggregated up to three, glossy black, subglobose, (289–)336–423(–482) μm high×(671–)677–724(–840) μm diam (mean=375×717, S.D. 76.6, 72.5, n1=5, n2=5). Necks central, elongated, straight to curved, (1,478–)1,525–2,671(–3,074) μm long (mean=2,208, S.D. 579.2, *n*=8). Asci ellipsoid to fusiform, apex papillate or rounded, stipe acute, apical ring conspicuous, (42–)45–50(–60)×18–20 μm (mean=49×20, S.D. 6.9, 2.8, n1=5, n2=2), ascospores arranged uniseriate to irregularly multiseriate. Ascospores fusiform, rounded ends, straight to slightly curved, one-septate, submedian, distinctly constricted at septum, each cell with 0–5 large guttules, (24–)25–28(–29)×4–5 μm (mean=26×4, S.D. 1.3, 0.2, n1=30, n2=28).

Habitat: On overwintered leaf blades, petioles, and veins of *Alnus nepalensis* D. Don (Betulaceae).

Distribution: China (Yunnan Province).

Notes: This is the only species of *Ophiognomonia* with an unusually thick perithecial cell wall. In addition, *O. apiospora* has the longest perithecial necks in the genus *Ophiognomonia.* This species has a distinct submedian septum that was also observed in ascospores of *O. alni-cordatae, O. gei-montani,* and *O. otanii.* This is only species of *Ophiognomonia* known to occur in China on the genus *Alnus*.

Ophiognomonia asiatica D.M. Walker & L.C. Mejía, sp. nov. Figure 9a–g.

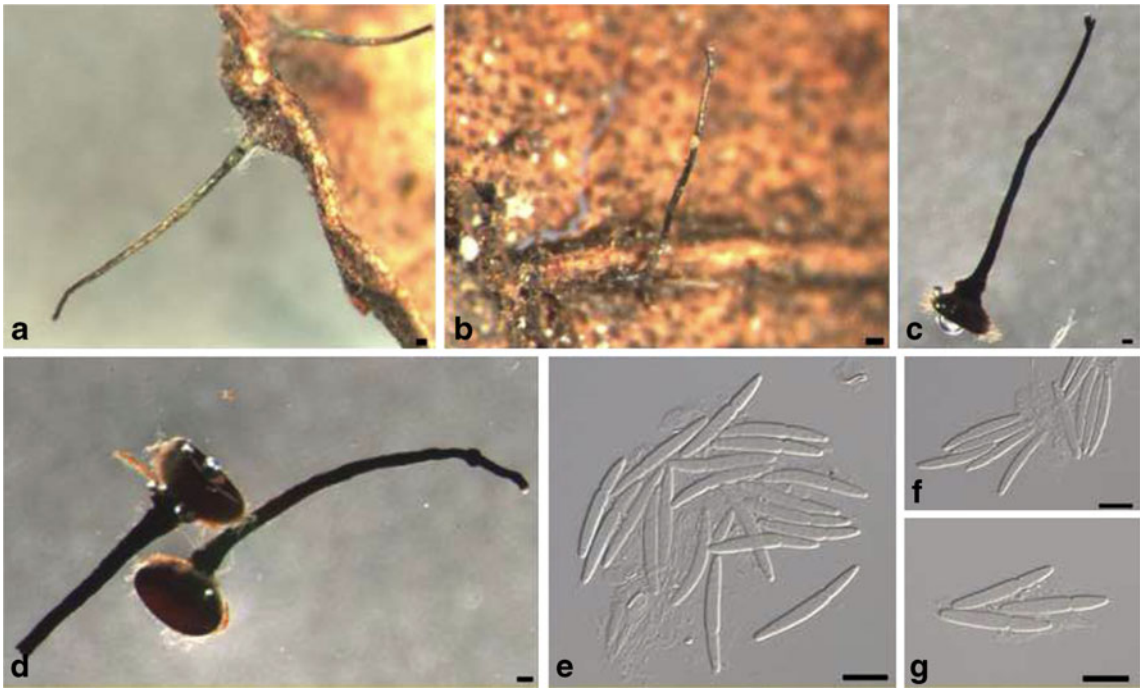

Fig. 8 *Ophiognomonia apiospora*. **a**–**g**. Holotype BPI 879601. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

MycoBank: MB 564081

Etymology: asiatica refers to the location where the holotype was collected.

Holotypus: JAPAN, IBARAKI: Tsukuba City, National Museum, on overwintered leaves of *Quercus serrata,* 2 April 2010, D.M. Walker (BPI 882231, ex-type culture DMW378.2=CBS 131351).

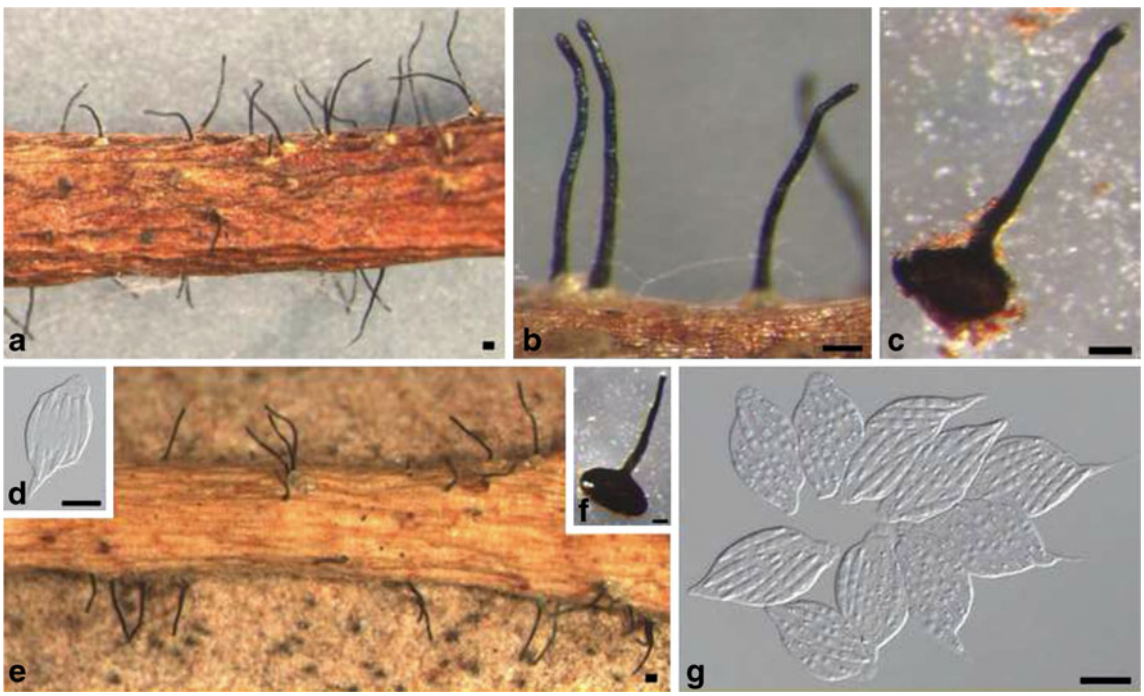

Fig. 9 *Ophiognomonia asiatica*. **a**–**c**. BPI 882225; **d**–**g**. Holotype BPI 882231. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf petioles, veins, and blades, solitary or aggregated up to three, glossy black, subglobose, (143–)154–263(–292) μm high×(239–)256–413(–514) μm diam (mean=212×345, S.D. 58, 91, n1=8, n2=8). Necks central, straight, curved, or sometimes sinuous, (438–)518–1,176(–1,225) μm long (mean=738, S.D. 178.7, *n*=23). Asci fusiform to ellipsoid, apex papillate, stipe long tapering, apical ring large, 3 μm diam, conspicuous, (24–)25–40(–41)×(10–)11–16(–17) μm (mean=31×14, S.D. 5.6, 1.8, n1=30, n2=25), ascospores arranged irregularly uniseriate, multiseriate, or parallel. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median or indistinctly supramedian, not constricted or slightly constricted at septum, each cell with 0–2 distinct guttules, (11–)12–15(–16)×2–3 μm (mean=14×2, S.D. 1.6, 0.4, n1=30, n2=30).

Habitat: On overwintered leaves of *Quercus aliena* Blume, *Quercus dentata* Thunb., and *Q. serrata* Murray (Fagaceae).

Distribution: China (Kunming) and Japan (Ibaraki prefecture).

Materials examined: CHINA, KUNMING: Kunming Botanical Garden, on overwintered leaves of *Quercus dentata*, 11 July 2008, L.C. Mejía (BPI 879600, LCM 500.01=CBS 131424). JAPAN, IBARAKI: Ushiku, Ushiku Nature Reserve, on overwintered leaves of *Quercus serrata,* 9 April 2010, D.M. Walker (BPI 882220, cultures DMW 351.3=CBS 131345, DMW 351.2); IBARAKI: Ushiku, Ushiku Nature Reserve, on overwintered leaves of *Quercus aliena,* 9 April 2010, D.M. Walker (BPI 882225, culture DMW361.1=CBS 131347).

Notes: This is the only species of *Ophiognomonia* known from both China and Japan on the genus *Quercus*. It is one of four species of *Ophiognomonia* known to occur exclusively on *Quercus.* A group of closely related species including *O. asiatica, O. kobayashii, O. otanii,* and *O. sogonovii* are specific to *Quercus* spp. and *Castanea* spp. within the Fagaceae (Fig. 2).

Ophiognomonia balsamiferae Sogonov, Stud. Mycol. 62: 51. 2008.

MycoBank: MB 512180

Habitat: On overwintered petioles of *Populus balsamifera* L. (Salicaceae).

Distribution: Canada (British Columbia).

Notes: This is the only species of *Ophiognomonia* known to occur on *Populus* in the Salicaceae. Ascospore appendages were observed in *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.* For a detailed description of this species, see Sogonov et al. (2008).

Ophiognomonia bugabensis L.C. Mejía & D.M. Walker, sp. nov. Figure 10a–g.

MycoBank: MB 564082

Etymology: bugabaensis refers to the district of Bugaba in Panama where the holotype was collected.

Holotypus: PANAMA, CHIRIQUI: District of Bugaba, Las Nubes, Parque Internacional La Amistad, main trail close to the gamewarden house in the entrance of the park, at 2225 masl on dead leaves of *Alnus acuminata,* 27 December 2006, L.C. Mejía, det. D.M. Walker (BPI 879256).

Perithecia immersed, on leaf blades and veins, hypophyllous, solitary to aggregated up to two, glossy black, subglobose, (178–)247–282(–303) μm high×(252–)275–474(–497) μm diam (mean=255×387, S.D. 48, 102, n1=5, n2=6). Necks central or marginal, straight, curved, or sinuous, (340–)349–559(–667) μm long (mean=461, S.D. 110, *n*=11). Asci obovoid to oval, apex rounded, stipe acute to rounded, (40–)43–55(–57)×(23–)25–26(–27) μm (mean=48×25, S.D. 7.7, 1.8, n1=5, n2=5), ascospores arranged irregularly uniseriate to multiseriate. Ascospores broadly fusiform, ends rounded, straight to slightly curved, one-septate, supramedian, slightly constricted at septum, (17–)18–19(–20)×(4–)5–6 μm (mean=18×5, S.D. 0.9, 0.6, n1=30, n2=17).

Habitat: On dead leaves or as an endophyte of *Alnus acuminata* Kunth (Betulaceae).

Distribution: Panama (Chiriqui).

Materials examined: PANAMA, CHIRIQUI: District of Bugaba, Las Nubes, Parque Internacional La Amistad, isolated as an endophyte from a twig of of *Alnus acuminata,* 22 December 2004, L.C. Mejía, det. D.M. Walker (culture LCM 362); CHIRIQUI: District of Bugaba, Las Nubes, Parque Internacional La Amistad, isolated as an endophyte from leaf of *Alnus acuminata,* 22 December 2004, L.C. Mejía, det. D.M. Walker (LCM 368=CBS 131399).

Notes: When compared to other species, *O. bugabensis* was isolated in high frequency as an endophyte of leaves and twigs of *Alnus acuminata* in Panama. This species was also collected on dead leaves of *Alnus acuminata* in Panama. This host plant occurs in montane cloud forest from Mexico to the Andes. Only *O. bugabensis* and *O. tucumanensis* are

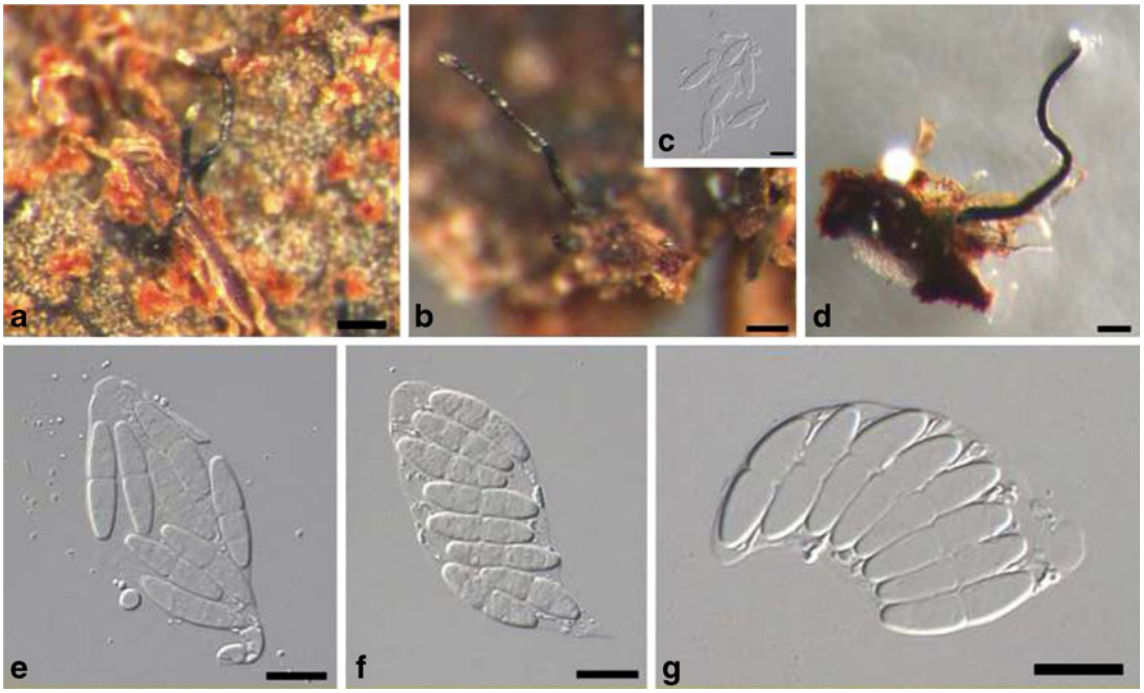

Fig. 10 *Ophiognomonia bugabensis*. **a**–**g**. Holotype BPI 879256. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

known to occur on *Alnus acuminata.* These two species can be distinguished by geographic location; also *O. bugabensis* has larger ascospores and shorter perithecial necks than *O. tucumanensis.* Interestingly, *O. bugabensis* was found at the same time of year when perithecia of another species of Gnomoniaceae, *Cryptosporella amistadensis*, is commonly found in the same geographic area.

Ophiognomonia clavigignenti-juglandacearum (Nair, Kostichka, & Kuntz) Broders & Boland, Fung. Biol. 115: 5. 2010.

Basionym: *Sirococcus clavigignenti-juglandacearum* Nair, Kostichka, & Kuntz, Mycologia 71: 643. 1979.

Habitat: Causing butternut canker of *Juglans ailantifolia* Carriére var. *cordiformis* (Makino) Rehder, *J. cinerea* L., and *J. nigra* L.

Distribution: Canada (New Brunswick, Ontario, Quebec) and United States (AK, CT, IN, MI, MN, MO, NC, NH, NY, OH, TN, VT, WI).

Notes: This species causes the devastating butternut canker disease in North America. It is known to occur only in the asexual state. For a detailed description of this species, see Broders and Boland (2010).

Ophiognomonia cordicarpa D.M. Walker, sp. nov. Figure 11a–h.

MycoBank: MB 564083

Etymology: cordicarpa refers to the heart-shaped perithecia of this species.

Holotypus: JAPAN, NAGANO: Ueda-shi, Sugadaira, waterfall at the Sugadaira Montane Research Center, on overwintered leaves of *Pterocarya rhoifolia,* 13 April 2010, D.M. Walker (BPI 882217, ex-type culture DMW 344.2= CBS 131342).

Perithecia immersed, occasionally causing host tissue to swell, on leaf blades and veins, solitary, glossy black, cordate to subglobose, 223–268 μm high×357–474 μm diam (mean=252×400, S.D. 25.4, 64.1, n1=3, n2=3). Necks central, lateral, or marginal, straight, curved, or sinuous, (672–)1,093–1,111(–1,117) μm long (mean= 998, S.D. 217.7, *n*=4). Asci narrowly fusiform, apex bluntly rounded, stipe acute or bluntly rounded, apical ring conspicuous, (69–)77–85(–92)×(7–)9–11(–13) μm (mean=82×10, S.D. 7.2, 1.9, n1=7, n2=7), ascospores arranged parallel to intertwined. Ascospores filiform with bluntly rounded ends, curved to sinuous, one-septate, supramedian, not constricted at septum, with many small guttules, (55–)56–77(–78)×1–2 μm (mean=64×1, S.D. 7.8, 0.4, n1=26, n2=20).

Habitat: On overwintered leaves of *Pterocarya rhoifolia* Siebold & Zucc. (Juglandaceae).

Distribution: Japan (Nagano prefecture).

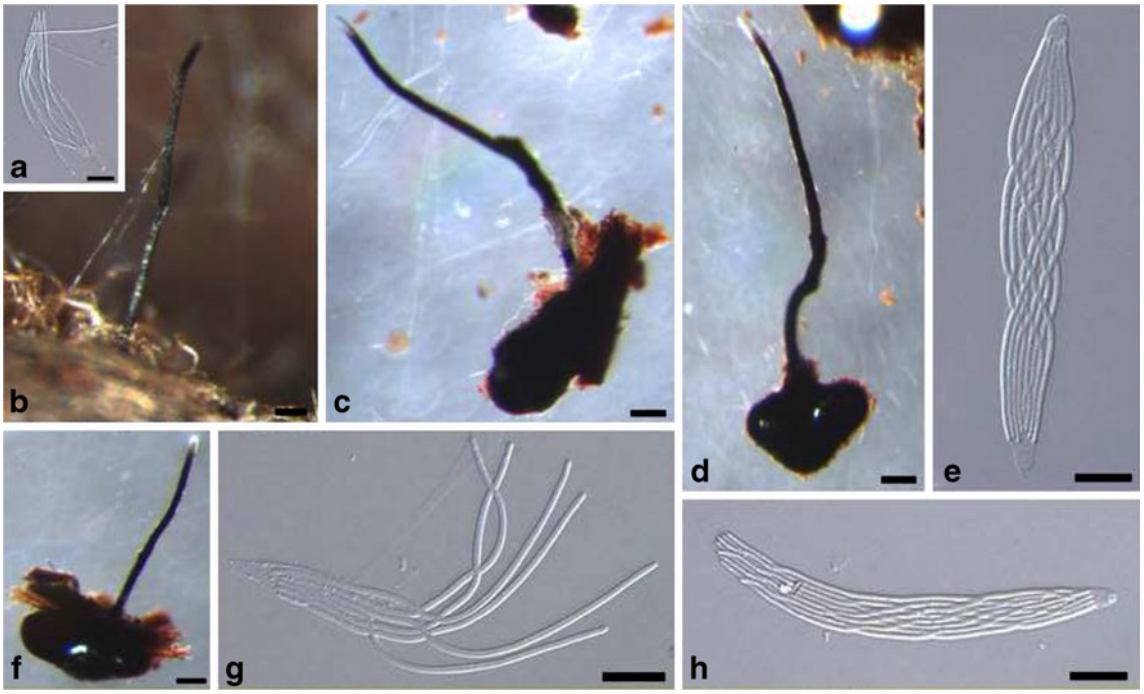

Fig. 11 *Ophiognomonia cordicarpa.* **a**–**h**. Holotype BPI 882217. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Notes: *Ophiognomonia cordicarpa* is one of 17 species known from Japan, and one of two known to occur on *Pterocarya* (Juglandaceae). Several other species are known to occur on *Carya* and *Juglans* (Juglandaceae) including the pathogens *O. leptostyla* and *O. clavigignenti-juglandacearum. Ophiognomonia cordicarpa* has long filiform ascospores, whereas *O. pterocaryae* has much shorter fusiform ascospores. The distinctive heart-shaped ascomata of this species is unusual for perithecia in *Ophiognomonia.* The species *O. cordicarpa, O. longispora, O. melanostyla,* and *O. sassafras* share elongated filiform ascospores and form a clade of closely related species (Fig. 3).

Ophiognomonia gardiennetii D.M. Walker, sp. nov. Figure 12a–g.

MycoBank: MB 564084

Etymology: gardiennetii refers to Alain Gardiennet to honor his contribution as a collector of many specimens of the Gnomoniaceae.

Holotypus: UNITED STATES, MICHIGAN: Mackinac County, Brevort campground, on overwintered leaves of *Alnus serrulata,* 27 May 2010, D.M. Walker (BPI 882262, ex-type culture DMW 469.3=CBS 131417).

Perithecia immersed to partially erumpent, occasionally causing host tissue to swell, on leaf blades, petioles, and veins, hypophyllous and epiphyllous, solitary, glossy black, subglobose, (178–)180–243(–253) μm high×(238–)248–309(–351) μm diam (mean=214×283, S.D. 29.9, 34, n1=9, n2=9). Necks central, marginal, or lateral, straight to curved, (356–)364–686(–697) μm long (mean=487, S.D. 131, *n*=15). Asci ellipsoid to fusiform, apex rounded to papillate, stipe acute to short tapering, (21–)24–34(–37)×(11–)12–15(–16) μm (mean=28×13, S.D. 3.4, 1.5, n1=21, n2=21), ascospores arranged uniseriate to irregularly multiseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, slightly to not constricted at septum, each cell with 0–2 distinct and several small guttules, (9–)10–12(–13)×2–3 μm (mean=11×3, S.D. 0.9, 0.3, n1=30, n2=30).

Habitat: On overwintered leaves of *Alnus serrulata* Willd. (Betulaceae).

Distribution: United States (MI).

Materials examined: UNITED STATES, MICHIGAN: Houghton County, FJ McClain State Park, on overwintered leaves of *Alnus serrulata,* 30 May 2010, D.M. Walker (BPI 882252, culture DMW 442.1=CBS 131409); MICHIGAN: Marquette County, hiking trail along Peshekee river, on overwintered leaves of *Alnus serrulata,* 30 May 2010, D.M. Walker (BPI 882276, culture DMW 513.1=CBS 131429).

Notes: Only *O. gardiennetii* and *O. trientensis* are known to occur exclusively on *Alnus* from the U.S. Morphologically these species are very similar and can only be distinguished

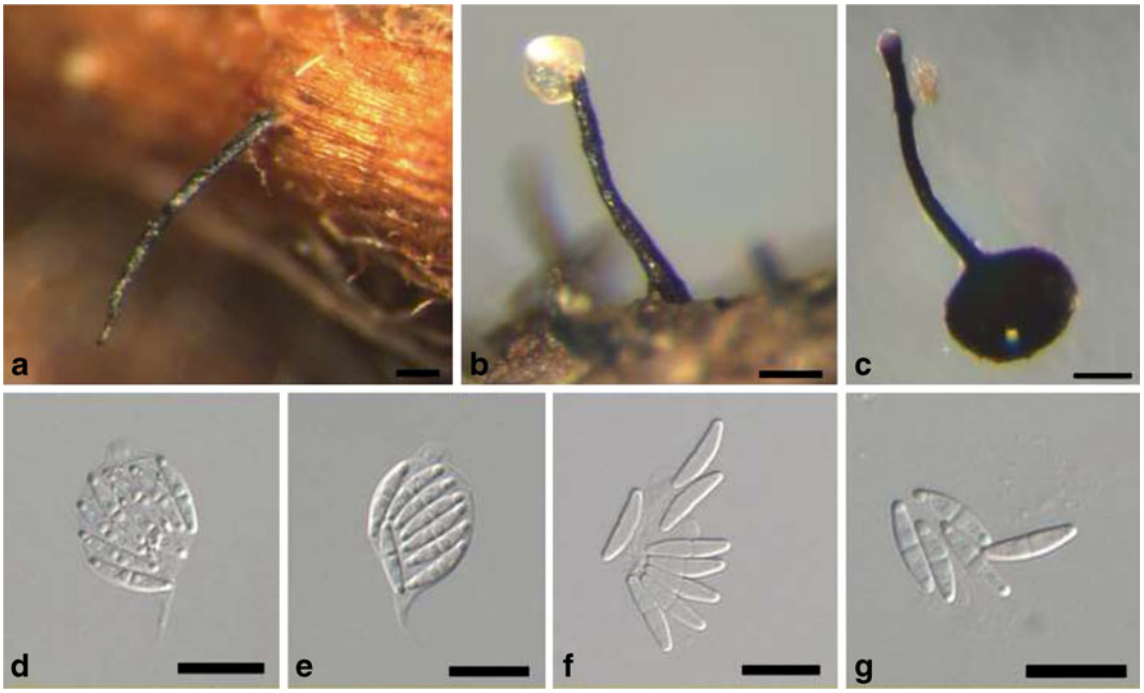

Fig. 12 *Ophiognomonia gardiennetii*. **a**. BPI 882252; **b**–**g**. BPI 882276. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

by DNA sequence data. In addition, they form a clade of closely related species with the butternut pathogen *O. clavigignenti-juglandacearum* (Fig. 4).

Ophiognomonia gei (Pat. & Doass.) D.M. Walker, comb. nov. Figure 13a–g.

Basionym: *Gnomonia gei* Pat. & Doass., in Patouillard, Tabl. analyt. Fung. France (Paris) 5: 214. 1886.

MycoBank: MB 564085

Perithecia immersed, causing host tissue to swell, bases visible under thin layer of host tissue, on herbaceous stems, leaves, or petioles, hypophyllous, solitary, glossy black, subglobose, 196–244 μm high×325–400 μm diam (mean=220×363, S.D. 34, 53, n1=2, n2=2). Necks central, long, straight to curved, (1,248–)1,451–1,784 μm long (mean=1,494, S.D. 270, *n*=3). Asci pyriform to clavate, apex rounded, stipe curved tapering, 24–36×4–6 μm (mean=35×5, S.D. 8.5, 1.4, n1=2, n2=2), ascospores arranged uniseriate. Ascospores fusiform, ends rounded, straight to slightly curved, one-septate, median to submedian, not constricted or slightly constricted at septum, each cell with several small guttules, with appendages at each end subulate to whip-shaped or absent, (15–)16–18(–19)×2 μm (mean=17×2, S.D. 1.1, 0.0, n1=11, n2=10).

Habitat: On overwintered leaves *Fragaria vesca* L. and *Geum pyrenaicum* Mill. (Rosaceae).

Distribution: Europe (France).

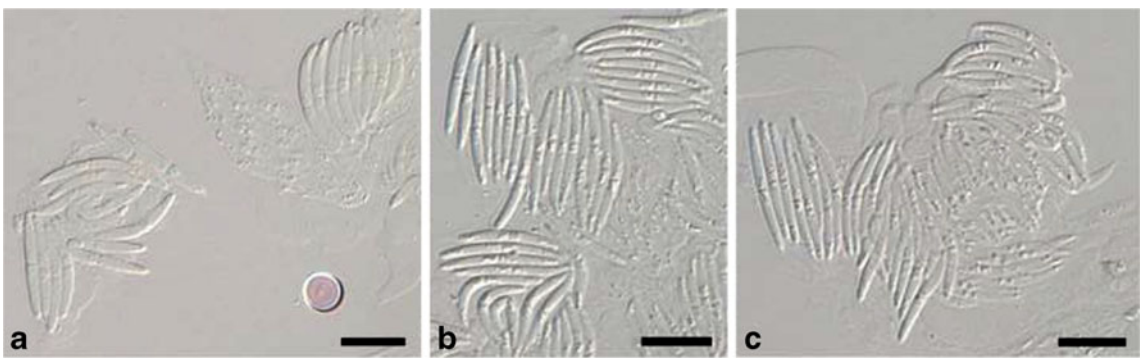

Fig. 13 *Ophiognomonia gei*. **a**–**c**. Lectotype Patouillard 5304. Scale bars of asci and ascospores=10 μm

Materials examined: FRANCE: *Geum pyrenaicum,* 26 June 1885, J.E. Doassans & N. Patouillard 5304 (LECTOTYPE of *Gnomonia gei* designated here, FH).

Notes: Ophiognomonia gei based on *Gnomonia gei* was originally collected in France on *Geum pyrenaicum.* Monod (1983) collected and isolated what he considered to be *Gnomonia gei* from Switzerland on *Fragaria vesca.* His description is in agreement with measurements taken from original material collected by Doassans and Patouillard in 1885 (FH 5304). Monod's specimen (Monod 301=culture CBS 818.79) was not available from LAU, however, the isolate was used here as a molecular representative of *O. gei.* This species is one of two that occur on *Geum,* and one of nine that occur on the host family Rosaceae. Of these species *O. gei, O. nipponicae, O. padicola, O. rosae, O. rubi-idaei* form a clade according to ITS sequence data (Fig. 5). Ascospore appendages were only observed in *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.*

Ophiognomonia gei-montani (Ranoj.) Sogonov, Stud. Mycol. 62: 58. 2008. Figure 14a–f.

Basionym: *Gnomonia gei-montani* Ranoj., Ann. Mycol. 8: 362. 1910.

MycoBank: MB 512183

Perithecia immersed, on leaf blades, petioles, and veins, causing swelling and rupture of host tissue, hypophyllous, solitary, glossy black, subglobose, (245–)315–331(–345) μm high×(300–)341–363(–383) μm diam (mean=309×347, S.D. 44.4, 35.6, n1=4, n2=4). Necks marginal, straight to curved, (289–)301–472(–530) μm long (mean=368, S.D. 84, *n*=9). Asci ellipsoid to fusiform, apex rounded, stipe tapering, apical ring not conspicuous, (39–)48–50(–56)×12–17 μm (mean=51×15, S.D. 4.2, 3.5, n1=3, n2=2), ascospores arranged irregularly uni- or biseriate. Ascospores fusiform, rounded ends, straight to slightly curved, one-septate, distinctly submedian, slightly to not constricted at septum, lacking guttules, (11–)13–14(–15)×(2–)3–4 μm (mean=14×3, S.D. 0.6, 0.3, n1=21, n2=18).

Habitat: On overwintered leaves of *Geum bulgaricum* Panc., *G. coccineum* Sm., *G. montanum* L., and *G. rhodopeum* Stoj. & Stef. (Rosaceae).

Distribution: Europe (Serbia, Switzerland).

Materials examined: SERBIA: on dead leaves of *Geum montanum,* 1910, N. Ranojević (S-F190027 HOLOTYPE of *Gnomonia gei-montani*); SWITZERLAND: Salvan, La Tendraz, 1,600 m, on dead leaves of *Geum montanum,* 28 May 2005, M. Monod (BPI 877589, GenBank EU 254872).

Notes: This species is one of two that occur on *Geum,* and one of nine that occur on the host family Rosaceae. A

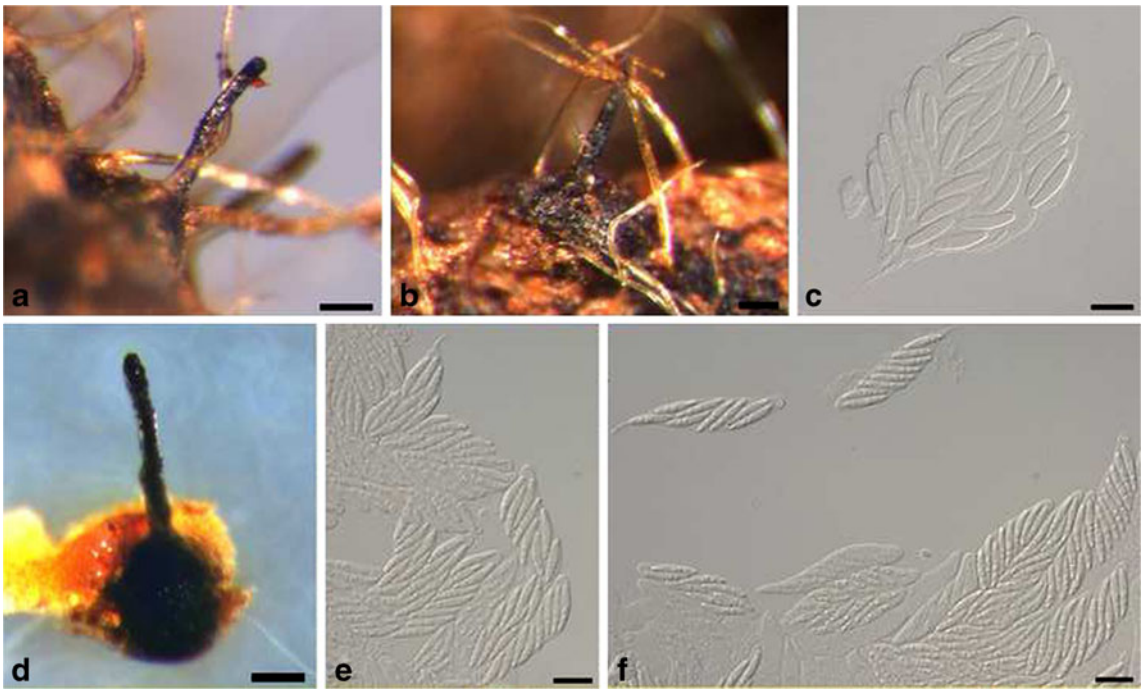

Fig. 14 *Ophiognomonia gei-montani*. **a**–**c**. BPI 877589; **d**–**f**. Holotype F 190027. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

distinct submedian septum was only observed in ascospores of four species including *O. alni-cordatae, O. apiospora, O. gei-montani,* and *O. otanii.*

Ophiognomonia gunmensis D.M. Walker, sp. nov. Figure 15a–g.

MycoBank: MB 564086

Etymology: gunmensis refers to the Japanese prefecture where the holotype of this species was collected.

Holotypus: JAPAN, GUNMA: Azuma, Azuma Nature Park, on overwintered leaves of *Quercus serrata,* 12 April 2010, D.M. Walker (BPI 882236, ex-type culture DMW 388.1=CBS 131401).

Perithecia immersed, on leaf blades and veins, epiphyllous or hypophyllous, solitary or up to two, glossy black, globose to subglobose, (108–)146–191(–220) µm high×(143–)146–244(–246) µm diam (mean=167×205, S.D. 37.1, 44.4, n1=7, n2=8). Necks central, short, straight, (230–)363–370(–390) µm long (mean=365, S.D. 52.1, *n*=8). Asci fusiform to ellipsoid, apex rounded, stipe acute, apical ring conspicuous, (26–)27–32(–42)×(8–)9–14(–15) µm (mean=30×12, S.D. 4.1, 2.2, n1=13, n2=13), ascospores arranged parallel or irregularly uniseriate to multiseriate. Ascospores fusiform, ends rounded, straight to slightly curved, one-septate, median to indistinctly supramedian, (14–)15–17(–18)×2 µm (mean=17×2, S.D. 0.9, 0.6, n1=30, n2=12).

Habitat: On overwintered leaves of *Quercus serrata* Murray (Fagaceae).

Distribution: Japan (Gunma prefecture).

Notes: Ophiognomonia gunmensis is one of 17 species from Japan, and one of four species known to occur specifically on *Quercus.* The perithecial necks are short relative to other species on *Quercus.*

Ophiognomonia hiawathae D.M. Walker, sp. nov. Figure 16a–g.

MycoBank: MB 564087

Etymology: hiawathae refers to the national park where this species was collected, which was named to honor the Native American leader of the Onondaga tribe, Hiawatha.

Holotypus: UNITED STATES, MICHIGAN: Mackinac County, Brevort campground, on overwintered leaves of *Betula lutea,* 27 May 2010, D.M. Walker (BPI 882261, ex-type culture DMW 466.1=CBS 131416).

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf blades and veins, solitary, glossy black, subglobose (183–)190–255(–261) µm high×(196–)200–261(–321) µm diam (mean=218×246, S.D. 33, 46, n1=6, n2=6). Necks central, straight to curved, (332–)368–696(–961) µm long (mean=569, S.D. 179, *n*=11).

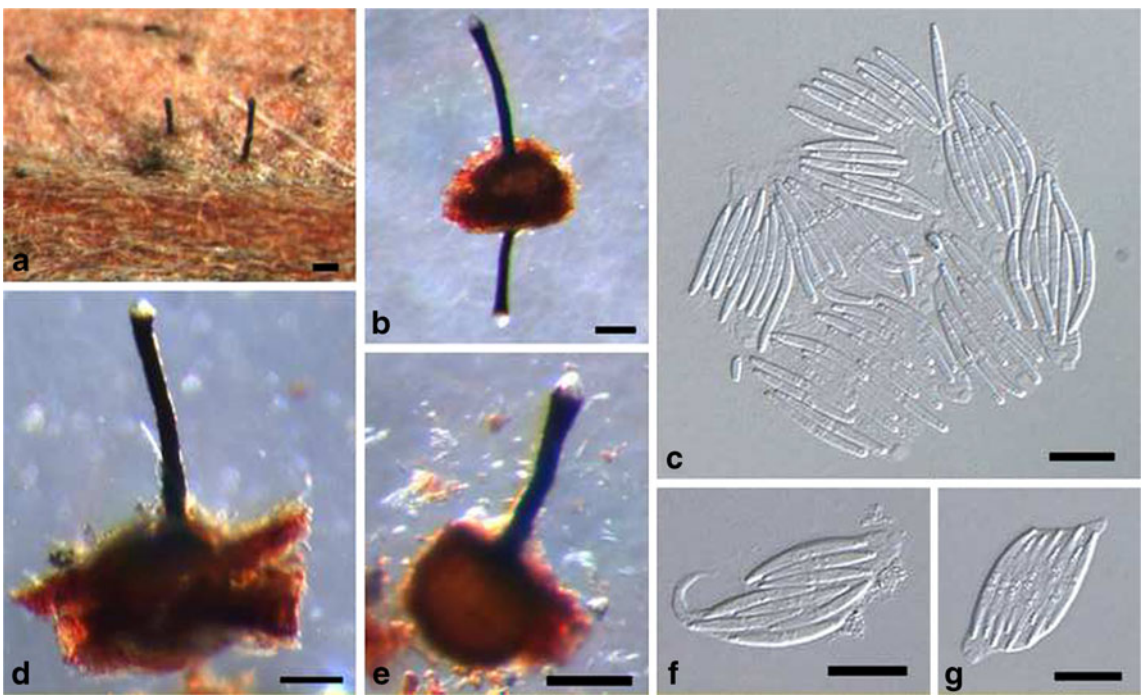

Fig. 15 *Ophiognomonia gunmensis*. **a**–**g**. Holotype BPI 882236. Scale bars of perithecia=100 µm. Scale bars of asci and ascospores=10 µm

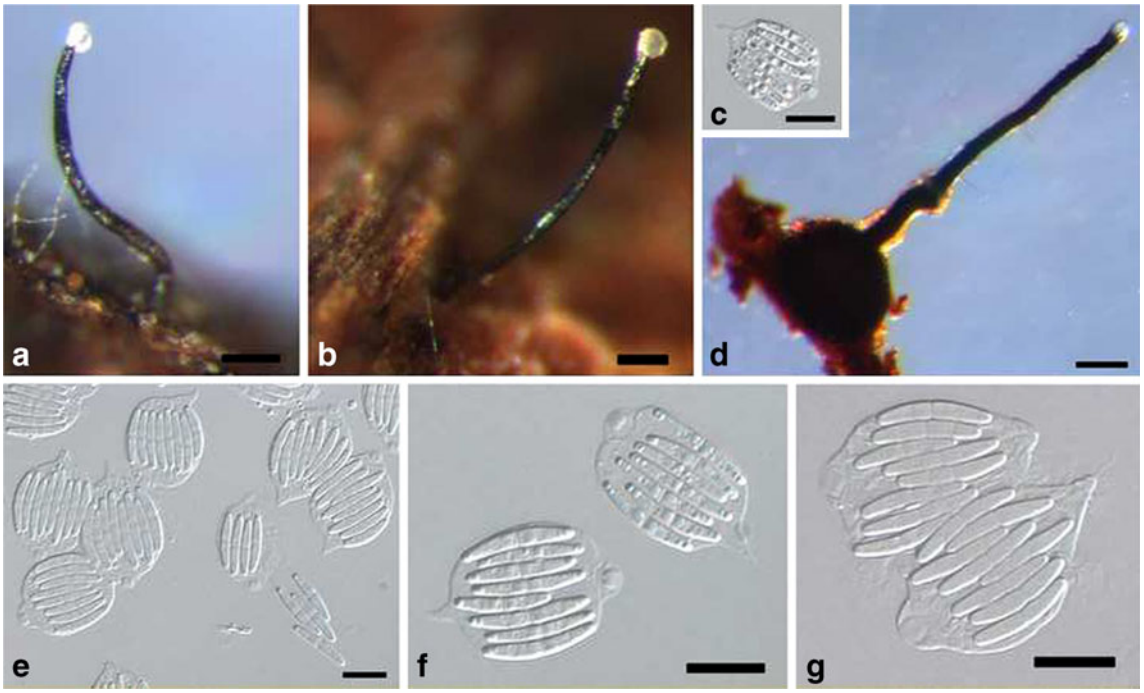

Fig. 16 *Ophiognomonia hiawathae*. **a**, **g**. BPI 882256; **b**–**f**. Holotype BPI 882261. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Asci fusiform to ellipsoid, apex papillate or rounded, stipe acute or tapering, apical ring conspicuous, (23–)24–33(–34)×(15–)16–19(–20) μm (mean=28×18, S.D. 2.7, 1.4, n1=22, n2=26), ascospores arranged parallel or irregularly uniseriate. Ascospores fusiform, ends rounded, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, slightly to not constricted at septum with appendages subulate, whip-shaped, or absent, (12–)13–15(–16)×2–3(–4) μm (mean=14×3, S.D. 0.9, 0.6, n1=30, n2=28).

Habitat: On overwintered leaves of *Betula lutea* Michx. (Betulaceae).

Distribution: United States (MI).

Materials examined: UNITED STATES, MICHIGAN: Schoolcraft County, Manistique, Hiawatha National Forest, Indian lake campground, on overwintered leaves of *Betula lutea,* 28 May 2010, D.M. Walker (BPI 882256, culture DMW 458.3=CBS 131413).

Notes: This species is similar to *O. michiganensis,* however, *O. hiawathae* has larger ascospores. *Ophiognomonia hiawathae* is one of four species of *Ophiognomonia* known to occur on *Betula* in the U.S. Ascospore appendages were only observed in *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.*

Ophiognomonia ibarakiensis D.M. Walker, sp. nov. Figure 17a–h.

MycoBank: MB 564088

Etymology: ibarakiensis refers to the Japanese prefecture where the holotype was collected.

Holotypus: JAPAN, IBARAKI: Hirasawa, rice fields at the foot of Mt. Tsukuba, on overwintered leaves of *Alnus* sp., 8 April 2010, D.M. Walker (BPI 882247, culture DMW 419.3=CBS 131405).

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf blades, petioles, and veins, solitary or aggregated up to three, glossy black, globose, (154–)171–186(–187) μm high×(161–)178–186(–187) μm diam (mean=176×178, S.D. 13.7, 12, n1=5, n2=4). Necks central to marginal, mostly straight or curved, tips occasionally hamate, (71–)153–545(–546) μm long (mean=335, S.D. 118.7, *n*=24). Asci fusiform to ellipsoid, apex rounded, stipe acute to short tapering, (23–)25–44(–50)×(10–)11–17(–19) μm (mean=32×14, S.D. 8.7, 2.6, n1=12, n2=12), ascospores arranged irregularly bi- to multiseriate. Ascospores ellipsoidal to oval, rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, not constricted at septum, (10–)11–12×3–4 μm (mean=11×4, S.D. 0.6, 0.6, n1=30, n2=30).

Habitat: On overwintered leaves of *Alnus* sp. (Betulaceae).

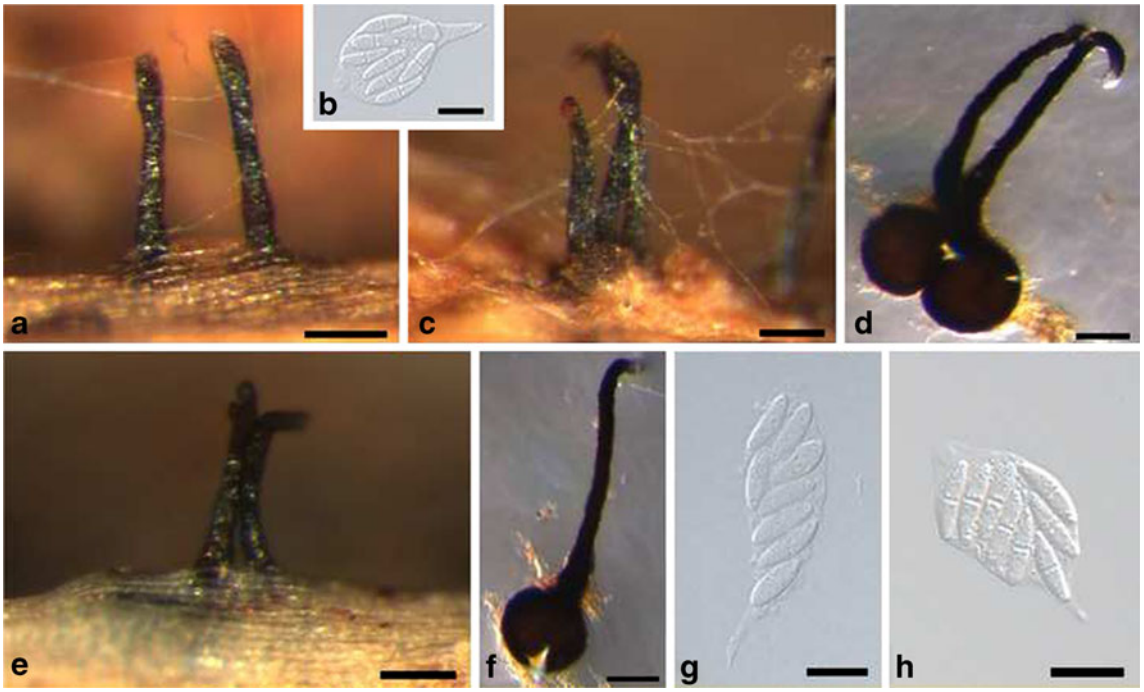

Fig. 17 *Ophiognomonia ibarakiensis*. **a**–**d**, **f**, **h**. Holotype BPI 882247; **e**, **g**. BPI 882227. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Distribution: Japan (Ibaraki prefecture).

Materials examined: JAPAN, IBARAKI: Hirasawa, rice fields at the foot of Mt. Tsukuba, on overwintered leaves of *Alnus* sp., 8 April 2010, D.M. Walker (BPI 882227, culture DMW 371.1=CBS 131349).

Notes: *Ophiognomonia ibarakiensis* is one of 17 species known from Japan, and one of four occuring on *Alnus* from this country. This species has slightly smaller ascospores than *O. naganoensis* and the ascospores overlap in size with *O. multirostrata,* which both occur on *Alnus* from Japan.

Ophiognomonia intermedia (Rehm) Sogonov, Stud. Mycol. 62: 58. 2008. Figure 18a–g.

Basionym: *Gnomonia intermedia* Rehm, Ann. Mycol. 6: 489. 1908.

=*Discula betulina* (Westend.) Arx, Verh. K. Akad. Wet., tweede sect. 51(3): 64. 1957.

=*Gloeosporidium betulinum* (Westend.) Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 125(1–2): 95. 1916.

=*Gloeosporium betulinum* Westend., Pl. crypt. exsicc. 19–20(nos 901–1000): no. 978. 1857.

MycoBank: MB 512185

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf blades and veins, epiphyllous or hypophyllous, solitary or in loose clusters, glossy black, globose to subglobose, (191–)207–250(–268) μm high× (195–)217–279(–331) μm diam (mean=228×261, S.D. 25.9, 46, n1=8, n2=8). Necks central, mostly straight, sometimes curved, (408–)464–1,047(–1,050) μm long (mean=678, S.D. 191, *n*=18). Asci fusiform to ellipsoid, apex papillate or rounded, apical ring not conspicuous, stipe acute to long tapering, (19–)20–41(–48)×(10–)11–16(–17) μm (mean=26.2×13.1, S.D. 8.7, 2.4, n1=18, n2=18), ascospores arranged parallel or irregularly uniseriate. Ascospores ellipsoid to fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, slightly to not constricted at septum with appendages at each end short, blunt, subulate or absent, (11–)12–14(–15)× 2–3 μm (mean=13×2, S.D. 0.8, 0.6, n1=30, n2=30).

Habitat: On overwintered leaves of *Alnus serrulata* Willd., *Betula lutea* Michx., *B. nana* L., *B. nigra* L., *B. papyrifera* Marshall, *B. pedula* Roth, and *B. pubescens* Ehrh. (Betulaceae).

Distribution: Canada (British Columbia), Europe (Germany, Scotland), Russia (Tver' and Novgorod provinces), and United States (MD, MI).

Materials examined: CANADA, BRITISH COLUMBIA: Agassiz, 15 km NE from Agassiz, route 7, on overwintered

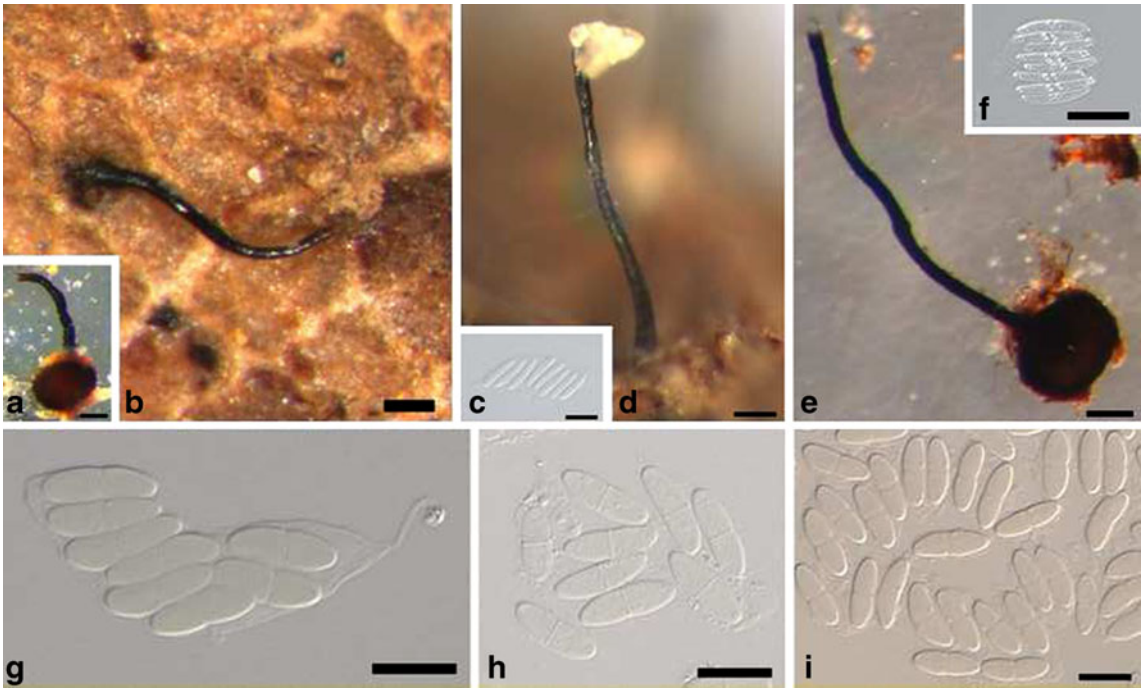

Fig. 18 *Ophiognomonia intermedia*. **a**–**b**, **g**–**i**. Lectotype Rehm 1794; **c**–**d**. BPI 882266; **e**–**f**. BPI 882267. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

leaves of *Betula papyrifera,* 13 May 2005, M.V. Sogonov (BPI 877599, GenBank EU 254884); BRITISH COLUMBIA: Burnaby, Burnaby Lake Regional Park, on overwintered leaves of *Betula papyrifera,* 12 May 2006, M.V. Sogonov (BPI 877602, GenBank EU 254886). GERMANY: *Betula* sp., 1908, Rehm (Rehm Ascomyceten 1794, BPI-bound, LECTOTYPE of *Gnomonia intermedia* designated here); SCOTLAND: Blair Atholl Estates, *Betula pendula,* 23 March 2005, S. Green (BPI 880534, EPITYPE of *Gnomonia intermedia* designated here, ex-epitype culture AR 4147=CBS 119188). RUSSIA, NOVGOROD PROVINCE: Kholm district, Rdeysky Natural Reserve, vicinity of the village Fryunino, on overwintered leaves of *Betula nana,* 11 June 2005, M.V. Sogonov (BPI 877496, GenBank EU 254881); NOVGOROD PROVINCE: Naberezhnaya reki Lovat' str., on overwintered leaves of *Betula pendula,* 23 August 2004, M.V. Sogonov (BPI 877498, GenBank EU 254878); TVER' PROVINCE: Toropets district, v. Kosilovo, on overwintered leaves of *Betula pendula,* 5 June 2005, M.V. Sogonov (BPI 877488B, GenBank EU 254887). UNITED STATES, MARYLAND: Prince George's County, Beltsville, Little Paint Branch Park, on overwintered leaves of *Betula nigra,* 17 March 2005, M.V. Sogonov (BPI 877597, GenBank EU 254879); MARYLAND: Prince George's County, Beltsville, Little Paint Branch Park, on overwintered leaves of *Betula nigra,* 11 April 2005, M.V. Sogonov (BPI 877598, GenBank EU 254880); MICHIGAN: Mackinac County, Cut River Bridge, on overwintered leaves of *Alnus serrulata,* 25 May 2010, D.M. Walker (BPI 882263, culture DMW 470.1=CBS 131418); MICHIGAN: Sanilac County, roadside south of Forestville, on overwintered leaves of *Betula papyrifera,* 27 May 2010, D.M. Walker (BPI 882266, culture DMW 482.2); MICHIGAN: Mackinac County, Brevort campground, on overwintered leaves of *Betula lutea,* 28 May 2010, D.M. Walker (BPI 882267, culture DMW 486.1=CBS 131421).

Notes: Ophiognomonia intermedia causes a foliar disease and dieback of young birch shoots (Green 2004). The anamorph/teleomorph connection between *Discula betulae* (Westend.) Pennycook and *O. intermedia* was documented by Green and Castlebury (2007). Ascospore appendages were observed in this species and *O. balsamiferae, O. gei, O. hiawathae, O. ischnostyla, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.*

Ophiognomonia ischnostyla (Desm.) Sogonov, Stud. Mycol. 62: 59. 2008. Figure 19a–j.

Basionym: *Sphaeria ischnostyla* Desm., Annals Sci. nat., Bot., sér. 3 11: 357. 1849.

≡ *Gnomonia ischnostyla* (Desm.) Auersw. in Gonn. & Rabenh., Mycol. Europ. 5/6: 2. 1869.

MycoBank: MB 512185

Perithecia immersed, occasionally causing host tissue to swell, on leaf petioles and veins, hypophyllous to

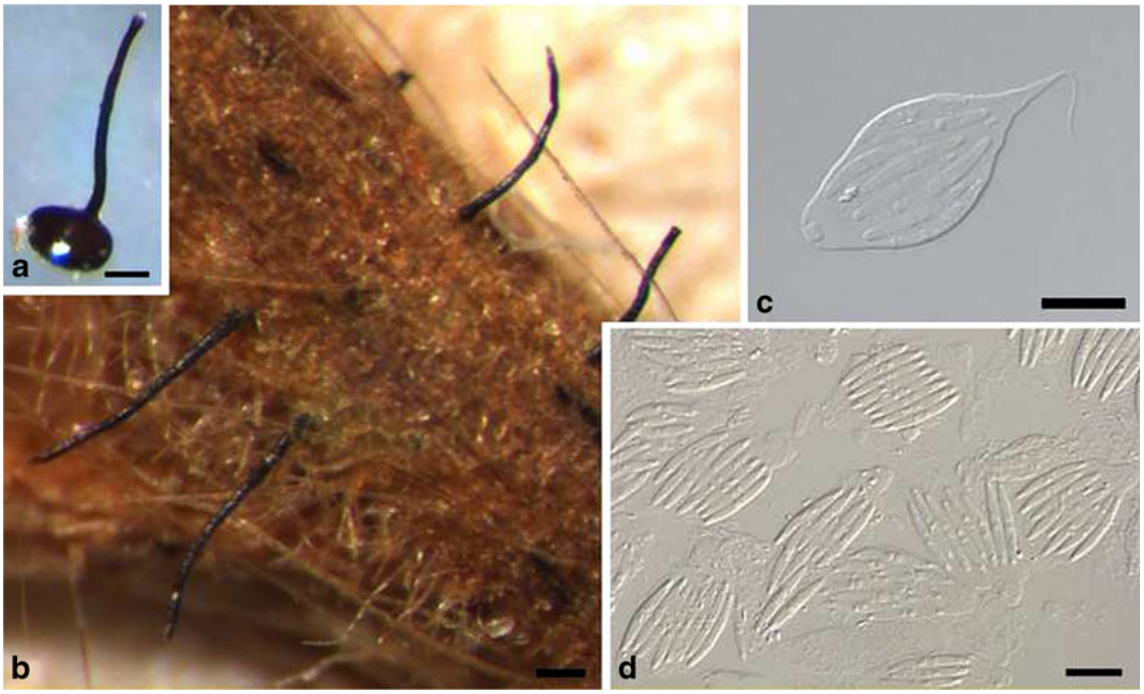

Fig. 19 *Ophiognomonia ischnostyla*. **a**–**b**, **d**. Lectotype Desmazieres, Pl. crypt. France 2084; **c**. BPI 871054B. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

epiphyllous, solitary or aggregated up to two, glossy black, globose to subglobose (137–)139–162(–166) μm high× (179–)200–212(–257) μm diam (mean=150×210, S.D. 13.2, 28.8, n1=5, n2=5). Necks central to marginal, mostly straight or curved to sinuous, occasionally swollen at the tip (350–)351–583(–590) μm long (mean=480, S.D. 83.7, *n*= 11). Asci fusiform, apex rounded, acute or long tapering stipe, apical ring conspicuous (30–)34–42(–46)×10–17 μm (mean=38×14, S.D. 7.3, 4.9, n1=4, n2=2), ascospores arranged parallel or irregularly uniseriate, fusiform, ends rounded, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, slight constriction at septum, appendages subulate to whip-shaped or absent (14–) 15–17(–18)×2–3 μm (mean=16×2, S.D. 1.4, 0.3, n1=30, n2=17).

Habitat: On overwintered leaves of *Carpinus betulus* L. and *Corylus avellana* L. (Betulaceae).

Distribution: Europe (France, Switzerland) and Russia (Novogorod Province).

Materials examined: FRANCE: *Carpinus betulus,* 1849, Desmazieres (Pl. Crypt. France 2084, BPI-bound, LECTOTYPE of *Sphaeria ischnostyla* designated here); RUSSIA, NOVOGOROD PROVINCE: Kholm district, Arboretum (Dendropark), near tree #560, on overwintered leaves of *Corylus avellana,* June 2005, M.V. Sogonov (BPI 877514B, EU 254899); SWITZERLAND: Ticino, Monte San Salvatore, on leaves of *Corylus avellana,* 28 May 2005, M.V. Sogonov (BPI 871054B, culture CBS 121234).

Notes: This species is morphologically similar to *O. pseudoischnostyla,* however, *O. ischnostyla* occurs on *Carpinus* spp. and *Corylus* spp., whereas *O. pseudoischnostyla* occurs on *Alnus* spp. and *Betula* spp. These two species both occur in Europe. Ascospore appendages were observed in *O. ischnostyla* and *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.* For a more detailed discussion on the taxonomy of this species, see Sogonov et al. (2008).

Ophiognomonia japonica D.M. Walker, sp. nov. Figure 20a–f.

MycoBank: MB 564089

Etymology: japonica refers to the host plant from which the holotype was collected.

Holotypus: JAPAN, GUNMA: Kawarayu, Kawarayu Trail, on overwintered leaves of *Prunus japonica,* 12 April 2010, D.M. Walker (BPI 882235, ex-type culture DMW 387.2= CBS 131355).

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf petioles and veins, solitary, glossy

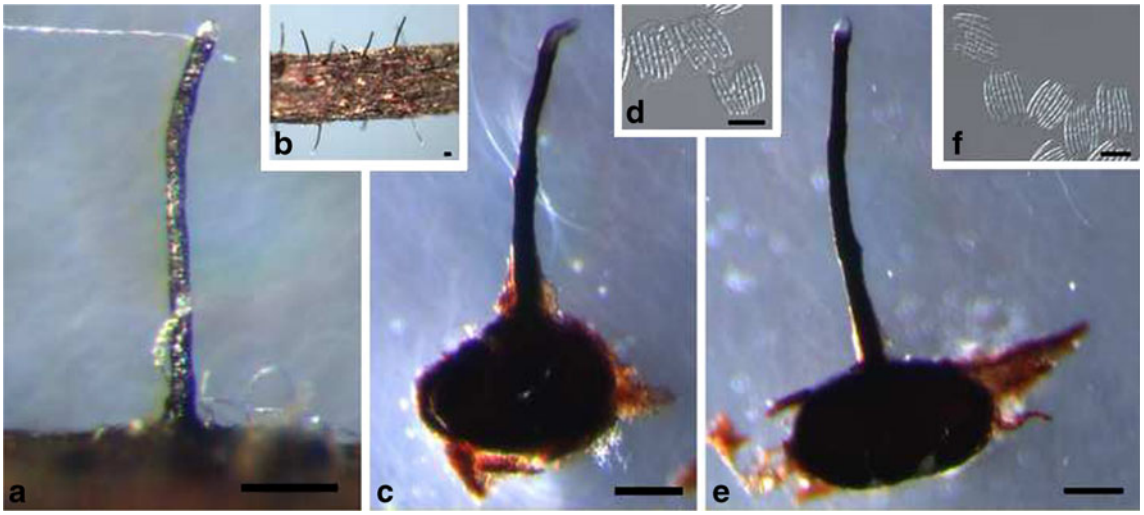

Fig. 20 *Ophiognomonia japonica*. **a**–**f**. Holotype BPI 882235. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

black, subglobose 175–222 μm high×(275–)325–340(–369) μm diam (mean=206×327, S.D. 27, 39.3, n1=3, n2=4). Necks central to marginal, mostly straight or slightly curved, (437–)462–613(–619) μm long (mean=540, S.D. 74.9, *n*=10). Asci fusiform to ellipsoid, apex papillate or rounded, stipe acute, tapering, or rarely whip-shaped, apical ring conspicuous, (20–)22–23(–25)×14–15 μm (mean=23×14, S.D. 2, 0.5, n1=11, n2=10), ascospores arranged parallel or uniseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly supramedian, not constricted at septum, (12–)13–16(–17)×2–3 μm (mean=14×2, S.D. 0.9, 0.2, n1=30, n2=19).

Habitat: On overwintered leaves of *Prunus japonica* Thunb. (Rosaceae).

Distribution: Japan (Gunma prefecture).

Notes: Ophiognomonia japonica is one of 17 species known from Japan and one of two occuring on *Prunus* from that country. This species has shorter perithecial necks and smaller ascospores than *O. nipponicae,* which also occurs on *Prunus* in Japan.

Ophiognomonia kobayashii D.M. Walker, sp. nov. Figure 21a–i.

MycoBank: MB 564090

Etymology: kobayashii was named after Takao Kobayashi to honor his contributions to the taxonomy of the Diaporthales of Japan.

Holotypus: JAPAN, IBARAKI: Tsukuba City, Natural Forest, on overwintered leaves of *Castanea crenata,* 4 April 2010, D.M. Walker (BPI 882232, ex-type culture DMW 379.3=CBS 131352).

Perithecia immersed, on leaf blades and veins, solitary, glossy black, globose to subglobose, (122–)127–169(–228) μm high×(124–)127–212(–217) μm diam (mean=151×170, S.D. 31.1, 36.9, n1=10, n2=10). Necks central, mostly straight, sometimes curved, (329–)400–645(–699) μm long (mean=493, S.D. 114.4, *n*=15). Asci fusiform to ellipsoid, apex papillate or rounded, stipe tapering, apical ring conspicuous, (20–)21–30(–31)×(10–)11–16(–17) μm (mean=26×14, S.D. 3.3, 1.8, n1=30, n2=30), ascospores arranged uniseriate or parallel, rarely multiseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly supramedian, slightly constricted at septum, each cell with one large and one small guttule, (11–)12–13(–14)×2–3 μm (mean=13×2, S.D. 0.9, 0.3, n1=30, n2=30).

Habitat: On overwintered leaves of *Castanea crenata* Siebold & Zucc. (Fagaceae).

Distribution: Japan (Ibaraki prefecture).

Materials examined: JAPAN, IBARAKI: Tsukuba City, Mt. Tsukuba, shrine trail, on overwintered leaves of *Castanea crenata,* 8 April 2010, D.M. Walker (BPI 882245, culture DMW 416.1=CBS 131403); IBARAKI: Tsukuba City, Natural Forest, on overwintered leaves of *Castanea crenata,* 4 April 2010, D.M. Walker (BPI 882229, culture DMW374.2=CBS 131350); IBARAKI: Ushiku, Ushiku Nature Reserve, on overwintered leaves of *Castanea crenata,* 9 April 2010, D.M. Walker (BPI 882218, culture DMW347.2=CBS 131343).

Notes: Ophiognomonia kobayashii is one of 17 species known from Japan and one of three occuring on *Castanea*

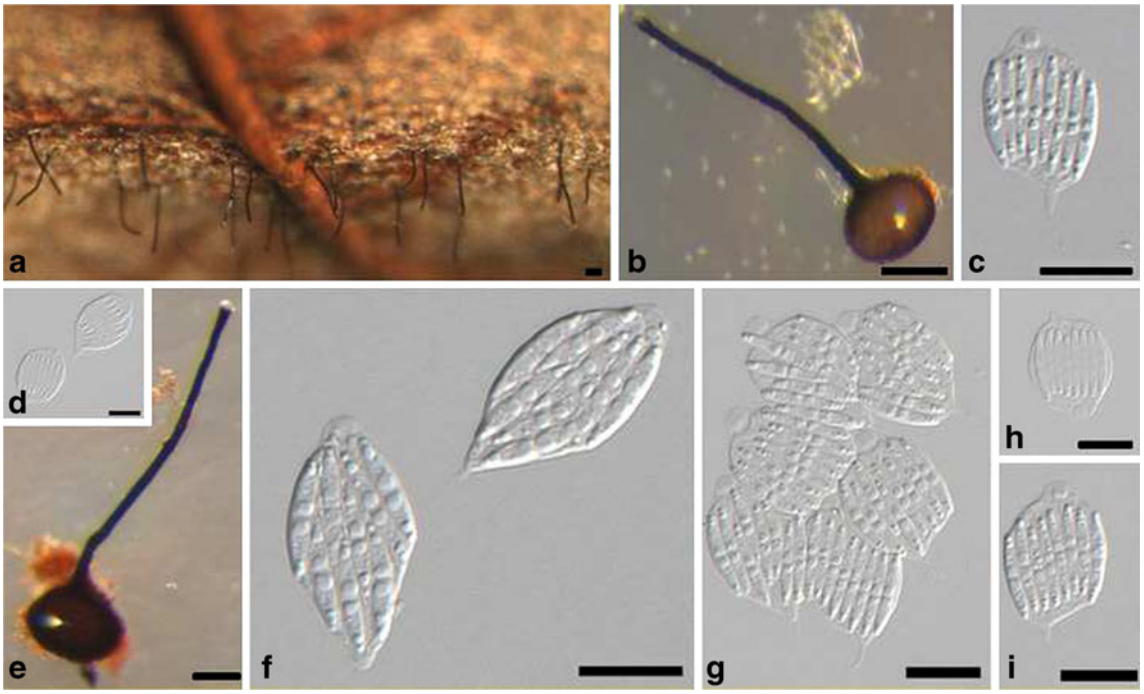

Fig. 21 *Ophiognomonia kobayashii*. **a**, **c**, **i**. BPI 882245; **b**, **g**–**h**. BPI 882229; **d**, **e**. Holotype BPI 882232; **f**. BPI 882218. Scale bars of perithecia = 100 μm. Scale bars of asci and ascospores = 10 μm

in that country. A group of closely related species including *O. asiatica, O. kobayashii, O. otanii,* and *O. sogonovii* are specific to *Quercus* spp. and *Castanea* spp. within the Fagaceae (Fig. 2).

Ophiognomonia lenticulispora D.M. Walker, sp. nov. Figure 22a–f.

MycoBank: MB 564091

Etymology: lenticulispora refers to the lens shaped ascospores of this species.

Holotypus: UNITED STATES, MARYLAND: Prince George's County, Beltsville Agricultural Research Center, on overwintered leaves of *Prunus* sp., 25 April 2011, D.M. Walker (BPI 882287, ex-type culture DMW 544 = CBS 131363).

Perithecia immersed, on leaf blades and veins, hypophyllous, solitary or loosely aggregated, glossy black, globose to subglobose, (189–)190–197(–204) μm high × (231–)235–263(–271) μm diam (mean = 195 × 250, S.D. 7, 20, n1 = 4, n2 = 4). Necks central to marginal, straight to slightly curved, (317–)323–327(–372) μm long (mean = 335, S.D. 25.2, *n* = 4). Asci ellipsoid to fusiform, apex rounded, stipe tapering, apical ring conspicuous, (28–)30–37(–39) × (12–)13–15(–17) μm (mean = 35 × 14, S.D. 3.5, 1.3, n1 = 11, n2 = 10), ascospores arranged irregularly uniseriate to biseriate. Ascospores oval to ellipsoid, rounded ends, straight, one-septate, median to indistinctly sub- or supramedian, slightly to not constricted at septum, one cell slightly larger than the other, each cell with several small guttules, (7–)8–9 × 3 μm (mean = 8 × 3, S.D. 0.6, 0.0, n1 = 30, n2 = 22).

Habitat: On overwintered leaves of *Prunus* sp. (Rosaceae).

Distribution: United States (MD).

Notes: Perithecia for this species only appeared on overwintered leaves after 2 weeks of incubation in a moist chamber at 4 °C in complete darkness. Only *O. lenticulispora* and *O. pseudoclavulata* have oval to ellipsoid ascospores in *Ophiognomonia*. These species can be distinguished from each other by ascospore shape, size, and presence/absence of appendages. *Ophignomonia lenticulispora* is one of two species of *Ophiognomonia* known to occur on *Prunus* in the U.S.

Ophiognomonia leptostyla (Fr.) Sogonov, Stud. Mycol. 62: 62. 2008. Figure 23a–n.

Basionym: *Sphaeria leptostyla* Fr., Syst. Mycol. 2: 517. 1823. ≡ *Gnomonia leptostyla* (Fr.) Ces & De Not., Comment. Soc. Crittog. Ital. 1(4): 232. 1863.

MycoBank: MB 512187

Teleomorph: Perithecia immersed, on leaf blades, petioles, and veins, causing host tissue to swell and rupture, hypophyllous, solitary or aggregated up to three, glossy black,

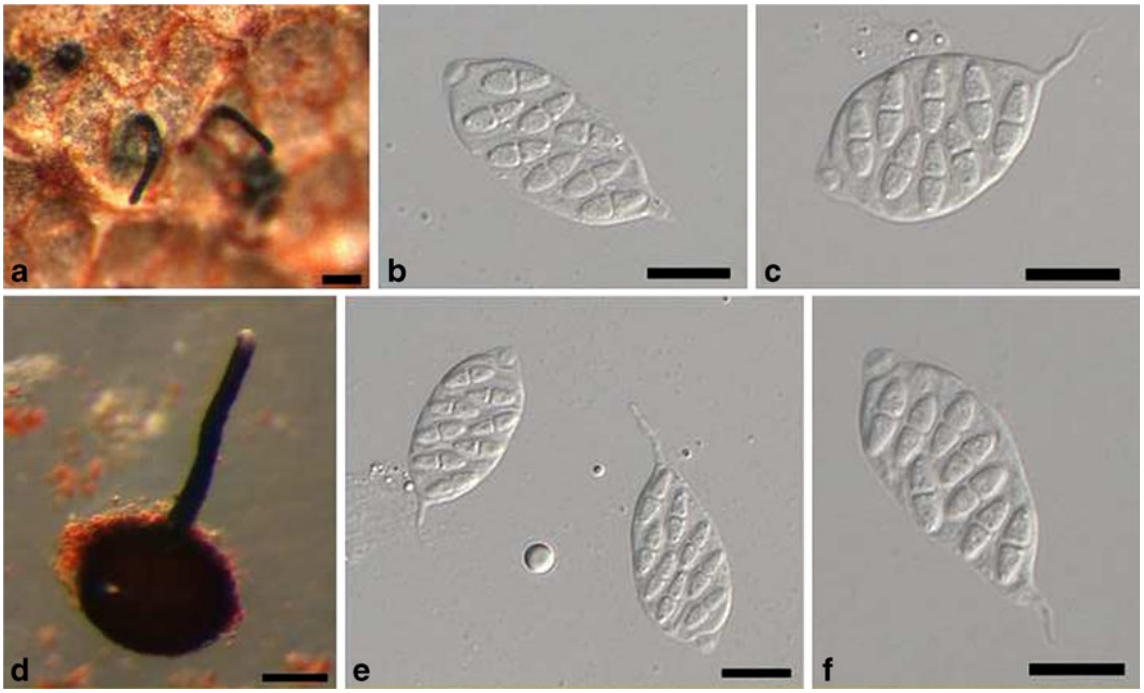

Fig. 22 *Ophiognomonia lenticulispora*. **a**–**f**. Holotype BPI 882287. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

subglobose, 175–252(–302) μm high×247–295(–309) μm diam (mean=243×284, S.D. 64, 32.5, n1=3, n2=3). Necks central, straight to curved, (240–)254–551(–601) μm long (mean=406, S.D. 150.3, *n*=7). Asci ellipsoid to fusiform, apex rounded, stipe short, tapering, apical ring conspicuous, (28–)29–30(–33)×(12–)15–16(–17) μm (mean=30×15, S.D. 2, 1.8, n1=8, n2=8), ascospores arranged irregularly uniseriate or parallel. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly supramedian, not constricted at septum, each cell with several small guttules, (13–)14–15×2 μm (mean=14×2, S.D. 0.6, 0.0, n1=27, n2=23).

Anamorph: Macroconidia lunate, reniform, or straight, basal cell bluntly rounded, apical cell with acute end, one-septate, median to indistinctly sub- or supramedian, distinctly constricted at septum, basal cell equal or larger than distal cell, hilum sometimes conspicuous, (22–)23–32(–35)×(6–)7–8(–9) μm (mean=28×7, S.D. 3.6, 1, n1=14, n2=16). Microconidia fusiform, ends rounded, aseptate, hilum sometimes conspicuous, (6–)9–12(–13)×2–3(–4) μm (mean=11×3, S.D. 2.7, 0.7, n1=7, n2=7).

Habitat: On living and overwintered leaves of *Juglans nigra* L., *Juglans regia* L., and *Juglans* sp. L. (Juglandaceae) causing leaf blotch.

Distribution: Canada (Ontario), Europe (Austria, Bulgaria, Germany, Poland, Russia, Switzerland), Iran, and United States (AL, DE, IA, IL, MA, MD, NY, PA, VA, WV).

Materials examined: BULGARIA: Sofia region, Zapaden Park, on overwintered leaves of *Juglans regia*, 5 June 2005, D. Stoykov (BPI 878231). UNITED STATES, PENNSYLVANIA: Centre County, State College, on symptomatic leaves of *Juglans regia,* 29 September 1919, L.O. Overholts (BPI 870007); WEST VIRGINIA: Monongalia County, Morgantown, on symptomatic leaves of *Juglans nigra,* 12 September 1928, W.A. Archer (BPI 611485).

Notes: Ophiognomonia leptostyla is the cause of the virulent disease called walnut anthracnose or walnut leaf blotch, which is prevalent in the Midwestern and Eastern United States (Neely and Black 1976; Berry 1981; Juhasova et al. 2006). This species has a broad geographic distribution in Europe, the Middle East, and North America. This is one of three species that occur on *Juglans.* Several other species are known to occur on *Carya* and *Juglans* in the Juglandaceae including the pathogen *O. clavigignenti-juglandacearum.*

Ophiognomonia longispora D.M. Walker, sp. nov. Figure 24a–j.

MycoBank: MB 564093

Etymology: longispora refers to the long ascospores of this species.

Holotypus: JAPAN, NAGANO: Ueda-shi, Sugadaira, arboretum at the Sugadaira Montane Research Center, on

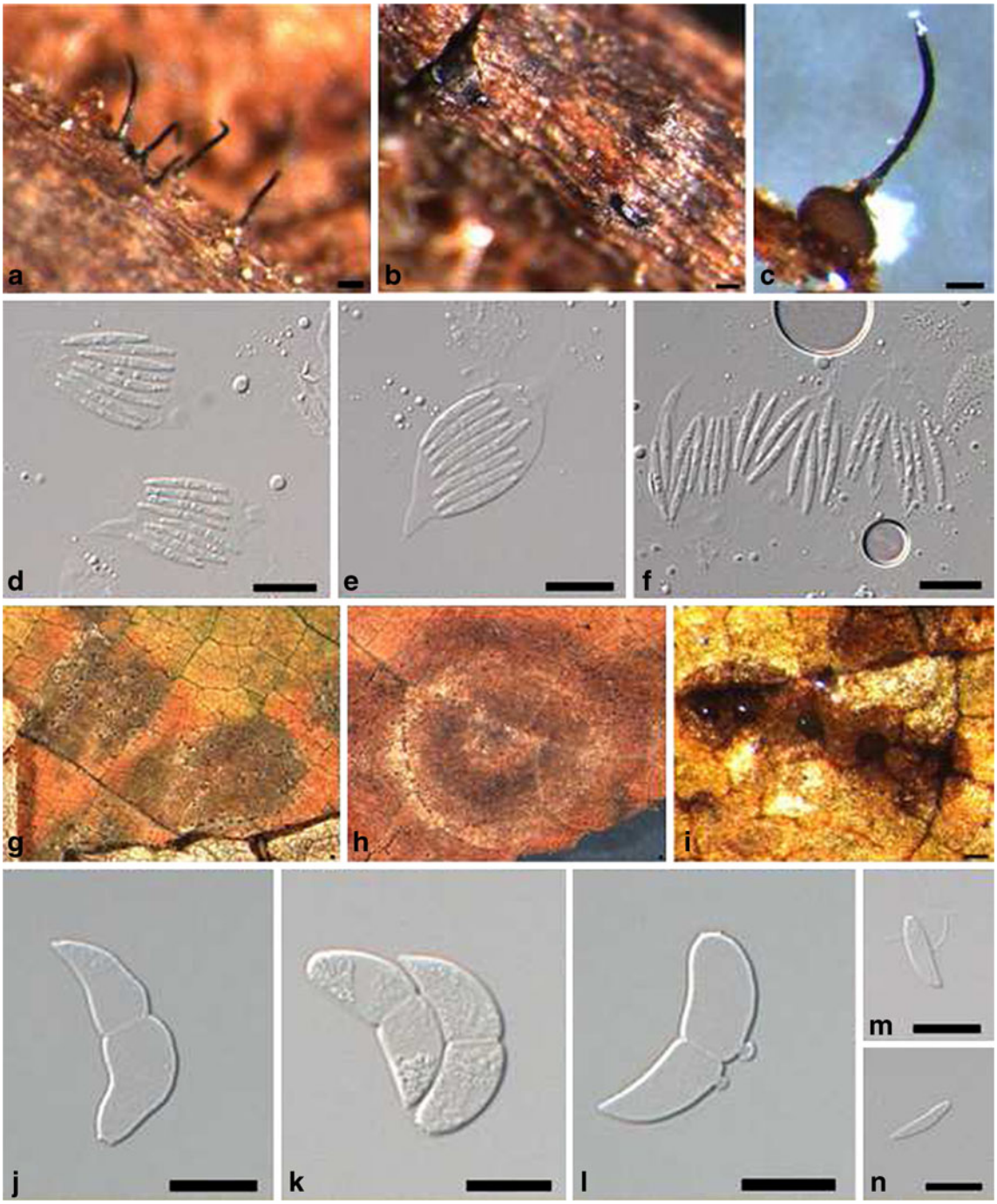

Fig. 23 *Ophiognomonia leptostyla*. **a**–**f**. BPI 878231; **g**, **i**–**j**, **l**, **n**. BPI 611485; **h**, **k**, **m**. BPI 870007. Scale bars of perithecia and disease leasions = 100 μm. Scale bars of all asci, ascospores, macro, and micro conidia = 10 μm

overwintered leaves of *Tilia maximowicziana,* 13 April 2010, D.M. Walker (BPI 882239, ex-type culture DMW 394.3 = CBS 131358).

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf blades and veins, epiphyllous or hypophyllous, solitary or aggregated up to two, glossy black, subglobose, (175–)177–256(–261) μm high × (218–)262–378(–380) μm diam (mean = 216 × 308, S.D. 40.6, 71.3, n1 = 6, n2 = 5). Necks central to marginal, straight, curved, or slightly sinuous, (305–)399–1,058(–1,090) μm long (mean = 795, S.D. 235, *n* = 17). Asci narrowly fusiform, apex acute to rounded, stipe acute, (49–)51–60(–62) × (5–)6–9(–10) μm (mean = 55 × 7, S.D. 4, 1.5, n1 = 11, n2 = 10), ascospores arranged parallel. Ascospores narrowly clavate, filiform or sinuous, rounded ends, straight to curved, one-septate, supramedian, basal cell narrower than distal cell,

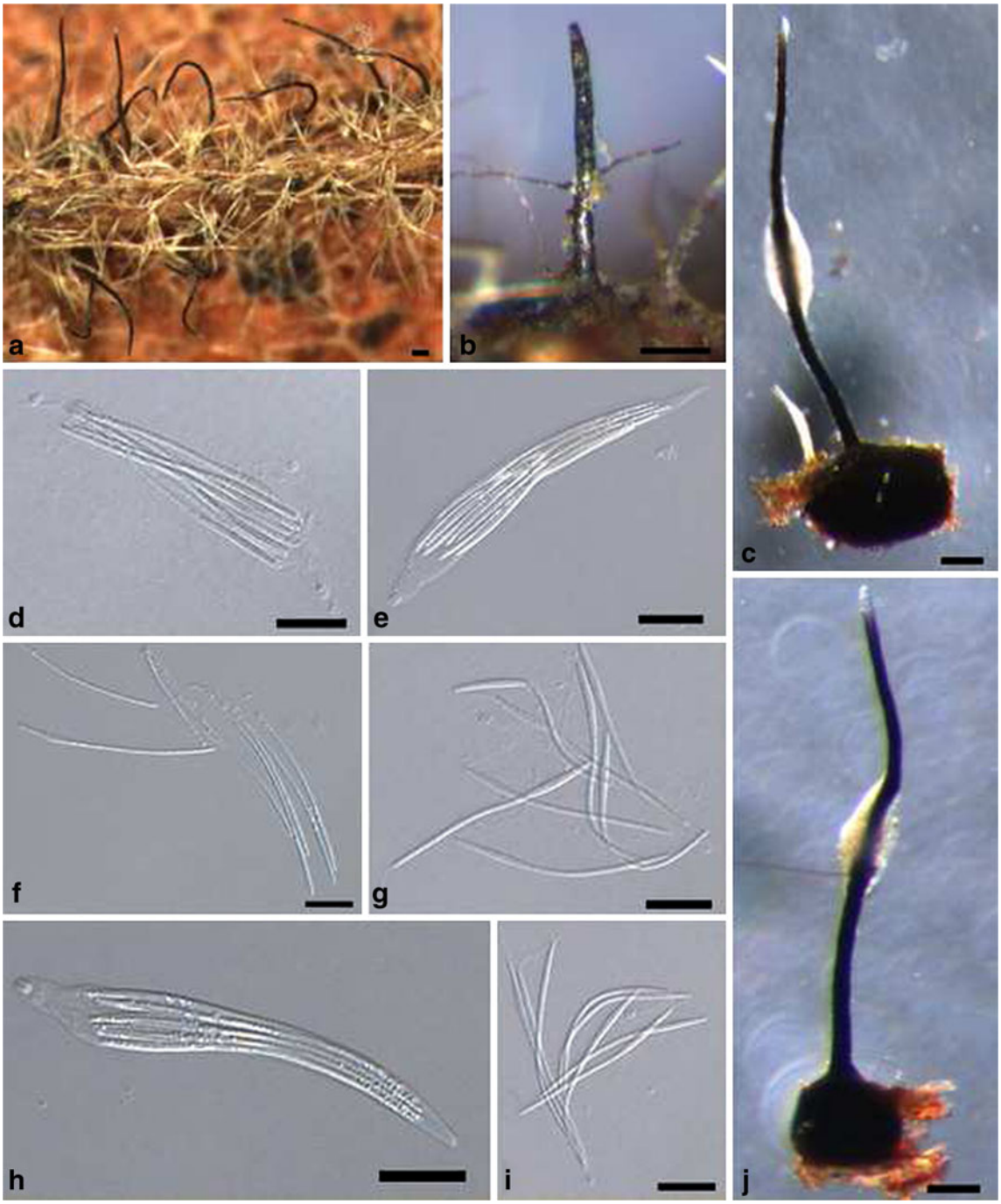

Fig. 24 *Ophiognomonia longispora*. **b**, **d**, **g**, **i**. BPI 882210; **a**, **c**, **e**–**f**, **h**, **j**. Holotype BPI 882239. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

with several small guttules, (33–)34–43(–44)×1–2 μm (mean=38×1, S.D. 3.2, 0.4, n1=30, n2=28) and appendages at each end subulate to whip-shaped.

Habitat: On overwintered leaves of *Tilia maximowicziana* Shiras. (Malvaceae).

Distribution: Japan (Nagano prefecture).

Materials examined: JAPAN, NAGANO: Ueda-shi, Sugadaira, Arboretum at the Sugadaira Montane Research Center, on overwintered leaves of *Tilia maximowicziana,* 13 April 2010, D.M. Walker (BPI 882210, culture DMW 325.4=CBS 131337).

Notes: *Ophiognomonia longispora* is one of 17 species known from Japan. In addition, this species is one of two

that occur on *Tilia* and the only species on this host genus from Japan. The species *O. cordicarpa, O. longispora, O. melanostyla,* and *O. sassafras* share elongated filiform ascospores. These species form a closely related clade (Fig. 3). Ascospore appendages were only observed in *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.*

Ophiognomonia maximowiczianae D.M. Walker, sp. nov. Figure 25a–e.

MycoBank: MB 564094

Etymology: maximowiczianae refers to the plant host epithet from which the holotype was collected.

Holotypus: JAPAN, NAGANO: Ueda-shi, Sugadaira, Arboretum at Sugadaira Montane Research Center, on overwintered leaves of *Betula maximowicziana,* 13 April 2010, D.M. Walker (BPI 882238, ex-type culture DMW 392.1= CBS 131357).

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf blades and veins, solitary, glossy black, subglobose, 188–253 μm high×207–287 μm diam (mean=221×247, S.D. 46, 56.6, n1=2, n2=2). Necks central, straight to curved, (517–)658–868(–1,010) μm long (mean=763, S.D. 218.8, *n*=4). Asci fusiform to ellipsoid, apex papillate or rounded, stipe acute or tapering, (23–)24–31(–33)×(11–)12–14(–15) μm (mean=28×13, S.D. 2.9, 1.1, n1=19, n2=15), ascospores arranged irregularly uniseriate to multiseriate. Ascospores fusiform, rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, not constricted at septum, (9–)10–11(–12)×2 μm (mean=11×2, S.D. 0.6, 0.0, n1=30, n2=30).

Habitat: On overwintered leaves of *Betula maximowicziana* Regel (Betulaceae).

Distribution: Japan (Nagano prefecture).

Notes: Ophiognomonia maximowiczianae is one of 17 species known from Japan, and the only species known to occur on *Betula* from that country.

Ophiognomonia melanostyla (DC.: Fr.) Berl., Icon. Fung. 2: 146. 1899. Figure 26a–h.

Basionym: *Sphaeria melanostyla* DC.: Fr., Fl. Franç. 5/6: 129. 1815: Syst. Mycol. 2: 517. 1823.

≡ *Gnomonia melanostyla* (DC.: Fr.) Auersw. in Gonn. & Rabenh., Mycol. Europ. 5/6: 28. 1869.

≡ *Gnomoniella melanostyla* (DC.: Fr.) Sacc., Syll. Fung. 1: 419. 1882.

≡ *Cryptoderis melanostyla* (DC.: Fr.) G. Winter, Rabenhorst's Kryptogamen Flora I, Abt. 2: 592. 1887.

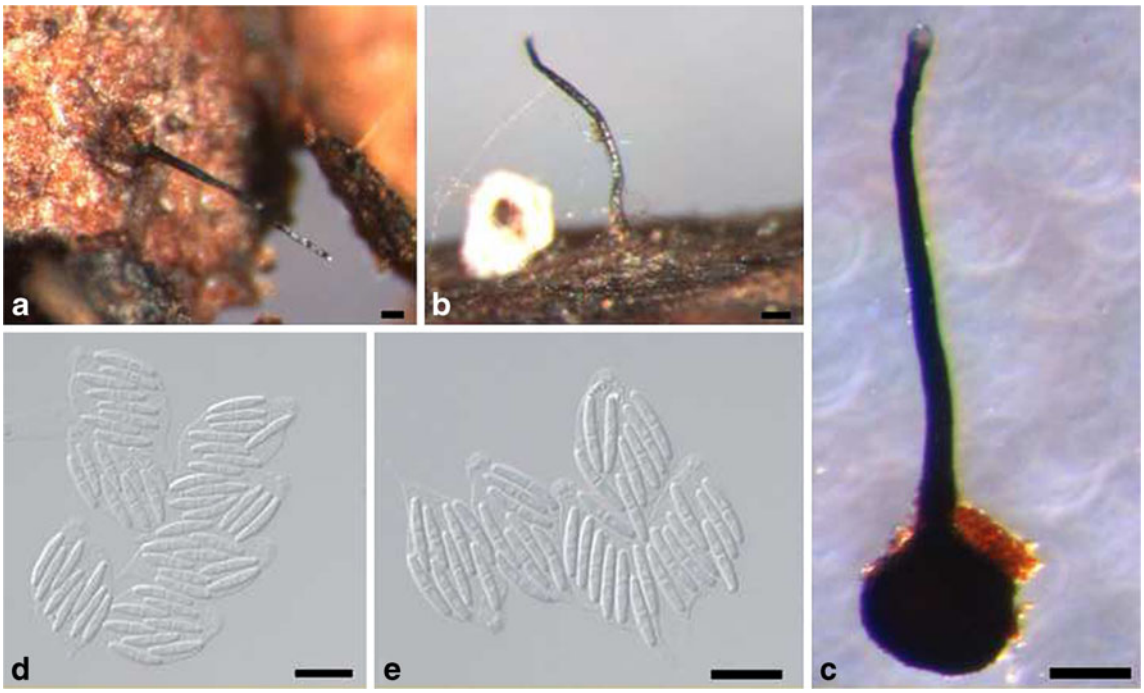

Fig. 25 *Ophiognomonia maximowiczianae*. **a**–**e**. Holotype BPI 882238. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

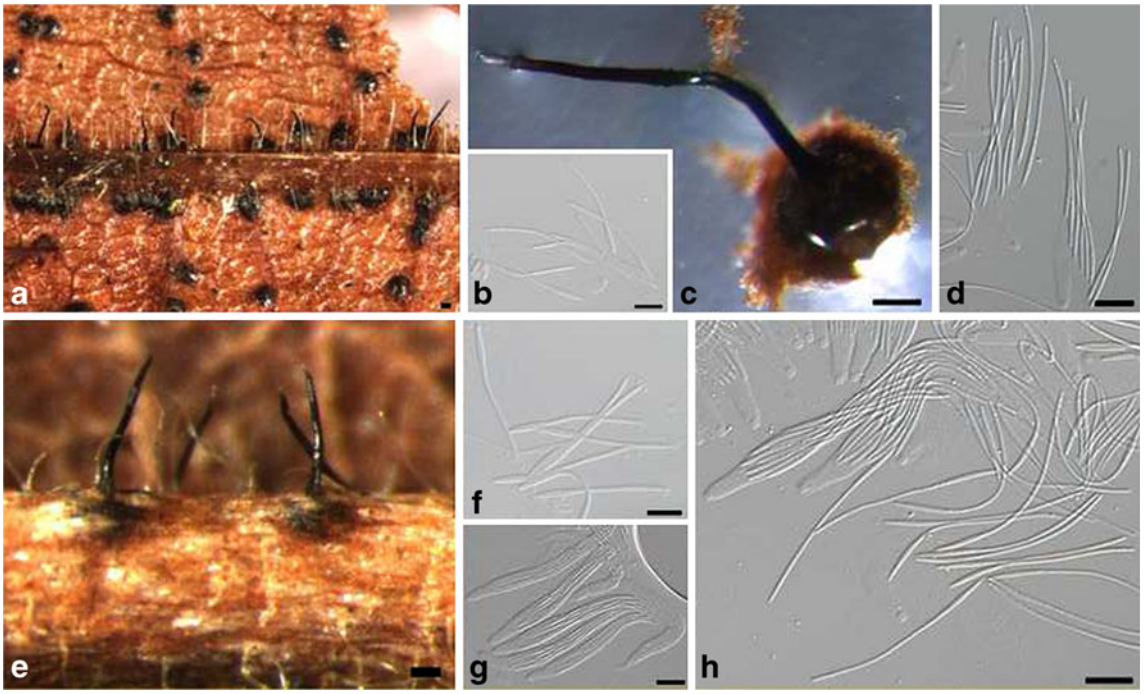

Fig. 26 *Ophiognomonia melanostyla*. **a**–**c**, **f**. Epitype BPI 882279; **d**, **g**–**h**. BPI 879257; **e**. BPI 882278. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Habitat: On overwintered leaves of *Tilia americana* L., *T. cordata* Mill., *T. heterophylla* Vent., and *Tilia* sp. L. (Malvaceae).

Distribution: Europe (Austria, Bulgaria, Czech Republic, France, Germany, Switzerland, Ukraine), Canada (Ontario), and United States (NY, PA).

Materials examined: FRANCE: Veronnes, on leaves of *Tilia* sp., 18 March 2011, A. Gardiennet (BPI 882278, culture DMW 522=CBS 131430); FRANCE: Le Mazeldan, Barre des Cevenes, on leaves of *Tilia* sp., Y. Mourgues & M. Chovillon (BPI 882279, EPITYPE designated here, ex-epitype culture DMW 533=CBS 131431); GERMANY: Frankfurt, Langen, on leaves of *Tilia heterophylla,* 2008, L.C. Mejía (BPI 879257, culture LCM 389.01=CBS 128482); SWITZERLAND: Vaud, Lausanne, Parc Bourge, on *Tilia cordata,* 28 May 2005, M.V. Sogonov (BPI 877611, GenBank EU 254913); SWITZERLAND: Vaud, St. Cergue, on *Tilia cordata,* 20 May 2005, M.V. Sogonov (BPI 877610, GenBank EU 254911). UNITED STATES, NEW YORK: Sullivan County, Roscoe vicinity, area around Campbell Inn, on *Tilia americana,* July 2005, M.V. Sogonov (BPI 877608, GenBank EU 254912).

Notes: This is the type species of *Ophiognomonia.* For a detailed description of this species, see Sogonov et al. (2008). The species *O. cordicarpa, O. longispora, O. melanostyla,* and *O. sassafras* share elongated filiform ascospores and form a clade of closely related species (Fig. 3). Ascospore appendages were observed for this species as well as in *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.*

Ophiognomonia michiganensis D.M. Walker, sp. nov. Figure 27a–l.

MycoBank: MB 564095

Etymology: michiganensis refers to the state where the holotype was collected.

Holotypus: UNITED STATES, MICHIGAN: Houghton County, FJ McClain State Park, on overwintered leaves of *Betula papyrifera,* 30 April 2010, D.M. Walker (BPI 882255, ex-type culture DMW 454.3=CBS 131412).

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf blades and veins, solitary, glossy black, globose to subglobose (141–)188–265(–287) μm high×(178–)214–341(–405) μm diam (mean=227×269, S.D. 34.5, 56.4, n1=16, n2=16). Occasionally two necks per base, necks central, straight or slightly curved, (228–)285–771(–879) μm long (mean=501, S.D. 191, *n*=20). Asci fusiform to ellipsoid, apex papillate or rounded, stipe tapering or occasionally acute to papillate, apical ring

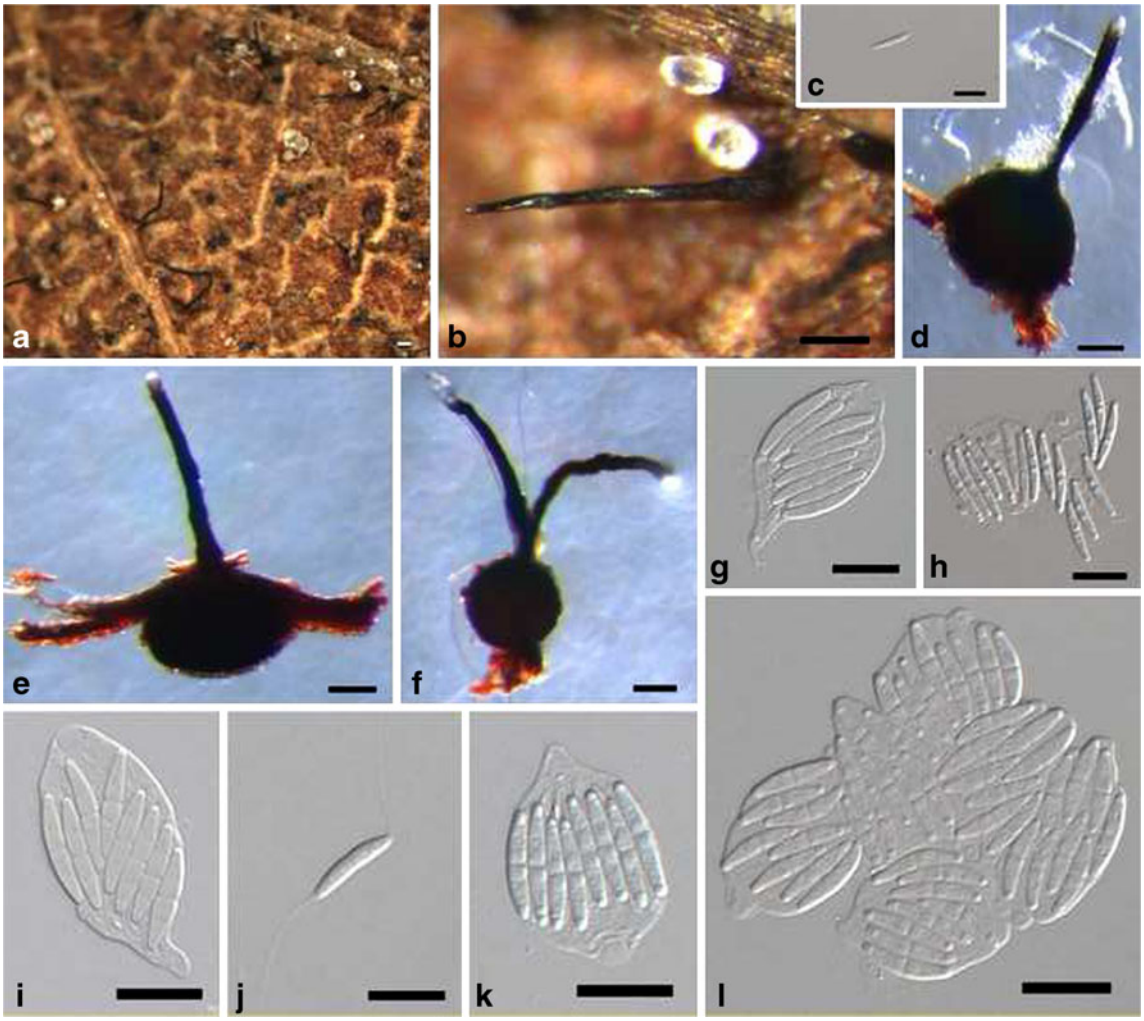

Fig. 27 *Ophiognomonia michiganensis.* **a**–**b**. BPI 882268; **c**–**d**, **f**, **h**. BPI 882273; **e**, **l**. BPI 882271; **i**, **k**, **g**. BPI 882268; **j**. BPI 882259. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

conspicuous (20–)23–34(–38)×(8–)11–17(–18) μm (mean=27×14, S.D. 4, 2, n1=30, n2=30), ascospores arranged parallel, irregularly uniseriate, or multiseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly submedian or distinctly submedian when on *Prunus* sp., slightly to not constricted at septum, (9–)10–14(–15)×2–3 μm (mean=12×2, S.D. 1.8, 0.4, n1=30, n2=30). Appendages subulate to whip-shaped or absent.

Habitat: On overwintered leaves of *Alnus serrulata* Willd., *Alnus* sp. Mill., *Betula alleghaniensis* Britton, *B. lutea* Michx., *B. papyrifera* Marshall, *Betula* sp., *Carpinus americana* Michx (Betulaceae), and *Prunus* sp. L. (Rosaceae).

Distribution: United States (MI, NC, NY).

Materials examined: UNITED STATES, MICHIGAN: Mackinac County, Brevort campground, on overwintered leaves of *Betula* sp., 28 May 2010, D.M. Walker (BPI 882273, culture DMW 508.3=CBS 131428); MICHIGAN: Mackinac County, Brevort campground, on overwintered leaves of *Betula papyrifera,* 27 May 2010, D.M. Walker (BPI 882254, culture DMW 451.2=CBS 131411); MICHIGAN: Mackinac County, Brevort campground, on overwintered leaves of *Prunus* sp., 27 May 2010, D.M. Walker (BPI 882271, culture DMW 505.3=CBS 131427); MICHIGAN: Mackinac County, Cut River Bridge, on overwintered leaves of *Betula papyrifera,* 28 May 2010, D.M. Walker (BPI 882259, culture DMW 464.1); MICHIGAN: Schoolcraft County, Manistique, Indian campground, on overwintered leaves of *Alnus serrulata,* 28 May 2010, D.M. Walker (BPI 882269, culture DMW 494.2=CBS 131423); MICHIGAN: Schoolcraft County, Manistique, Indian campground, on overwintered leaves of *Betula lutea,* 28 May 2010, D.M. Walker (BPI 882260, culture DMW 465.2=CBS 131415); MICHIGAN: Roscommon County, Marl Lake, on overwintered leaves of *Betula papyrifera,*

27 May 2010, D.M. Walker (BPI 882258, culture DMW 461.2=CBS 131414); MICHIGAN: Alger County, Miners Falls, on overwintered leaves of *Betula lutea,* 31 May 2010, D.M. Walker (BPI 882253, culture DMW447.1=CBS 131410); MICHIGAN: Sanilac County, roadside park south of Forestville, on overwintered leaves of *Alnus* sp., 27 May 2010, D.M. Walker (BPI 882264, culture DMW 475.1= CBS 131419); MICHIGAN: Alger County, Sable Falls, on overwintered leaves of *Alnus serrulata,* 29 May 2010, D.M. Walker (BPI 882268, culture DMW492.1=CBS 131422); MICHIGAN: Alger County, Sable Falls, on overwintered leaves of *Betula papyrifera,* 29 May 2010, D.M. Walker (BPI 882265, culture DMW478.1=CBS 131420); NEW YORK: Franklin County, Adirondack High Peaks Region, Marcy Dam, on leaves of *Betula alleghaniensis,* 9 June 2007, L.C. Mejía (BPI 881487, culture LCM 161); NORTH CAROLINA: Haywood County, Great Smoky Mountains National Park, Cataloochee, beginning of the trail, on overwintered leaves of *Betula lenta,* 23 May 2006, M.V. Sogonov (BPI 877624); NORTH CAROLINA: Haywood County, Great Smoky Mountains National Park, Cataloochee, beginning of the trail, on overwintered leaves of *Carpinus americana,* 23 May 2006, M.V. Sogonov (BPI 877467B, culture CBS 121908).

Notes: This species is very common in the Eastern and Midwestern U.S. on several genera in the Betulaceae. *Ophiognomonia setacea* and *O. michiganensis* are the only species of *Ophiognomonia* that occur on more than one plant family or order. Ascospore appendages were observed in *O. michiganensis* as well as *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. melanostyla, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.* Multiple-necked perithecia were occasionally observed in *O. michiganensis* and *O. multirostrata,* a phenomenon often occurring in culture, but rarely in nature for species of *Gnomoniopsis* (Walker et al. 2010) and *Ophiognomonia.*

Ophiognomonia micromegala (Ellis & Everh.) Sogonov, Stud. Mycol. 62: 63. 2008. Figure 28a–j.

Basionym: *Diaporthe micromegala* Ellis & Everh., Proc. Acad. nat. Sci. Philad. 45: 449. 1894.

≡ *Plagiostoma micromegalum* (Ellis & Everh.) M.E. Barr, Mycol. Mem. 7: 112. 1978.

MycoBank: MB 512188

Perithecia immersed, occasionally causing host tissue to swell, on leaf rachises and veins, solitary or aggregated 2–3, glossy black, globose to subglobose, (209–)227–379(–399) μm high×(351–)388–478(–491) μm diam (mean=311×440, S.D. 59.1, 57.4, n1=13, n2=13). Necks central to marginal, straight to curved, (223–)227–537(–624) μm long (mean= 384, S.D. 121.8, *n*=17). Asci fusiform, apex rounded, stipe short tapered or rounded, apical ring conspicuous, (51–)61–70×(16–)18–20 μm (mean=61×18, S.D. 9.5, 2, n1=3, n2= 3), ascospores arranged irregularly parallel or multiseriate. Ascospores fusiform to broadly fusiform with bluntly rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, slightly to distinctly constricted at septum, each cell with many large and small distinct guttules, (26–)27–50(–53)×(3–)4–11(–12) μm (mean= 40×7, S.D. 8.8, 3.5, n1=30, n2=30).

Habitat: On overwintered leaves and rachises of *Carya* sp. Nutt. (Juglandaceae).

Distribution: United States (MD).

Materials examined: UNITED STATES: *Carya* sp., 21 August 1893, A. Commons (Commons 2309, ISOTYPE of *Diaporthe micromegala,* NY); MARYLAND: Prince George's County, Beltsville Agricultural Reseach Center, on overwintered leaves and rachises of *Carya* sp., 21 April 2011, D.M. Walker (BPI 882280, EPITYPE designated here, ex-epitype culture DMW 535=CBS 131432); MARYLAND: Prince George's County, Beltsville Agricultural Research Center, on overwintered leaves and rachises of *Carya* sp., 21 April 2011, D.M. Walker (BPI 882281, culture DMW 536= CBS 131433).

Notes: Ophiognomonia micromegala has large fusiform ascospores unlike the narrowly fusiform ascospores of *O. melanostyla. Ophiognomonia micromegala* is one of seven species that occur on plants in the Juglandaceae, and one of two that occur on *Carya* in the U.S.

Ophiognomonia monticola D.M. Walker, sp. nov. Figure 29a–g.

MycoBank: MB 564096

Etymology: monticola refers to Mt. Tsukuba where the holotype was collected.

Holotypus: JAPAN, IBARAKI: Tsukuba City, west side of Mt. Tsukuba, on overwintered leaves of *Carpinus* sp., 5 April 2010, D.M. Walker (BPI 882222, ex-type culture DMW 357.3=CBS 131346).

Perithecia immersed, occasionally causing host tissue to swell, on leaf blades, petioles, and veins, solitary or aggregated up to two, glossy black, globose, subglobose, or ellipsoidal, (88–)109–123(–146) μm high×(110–)154–232 (–247) μm diam (mean=121×184, S.D. 23.4, 56.3, n1=5,

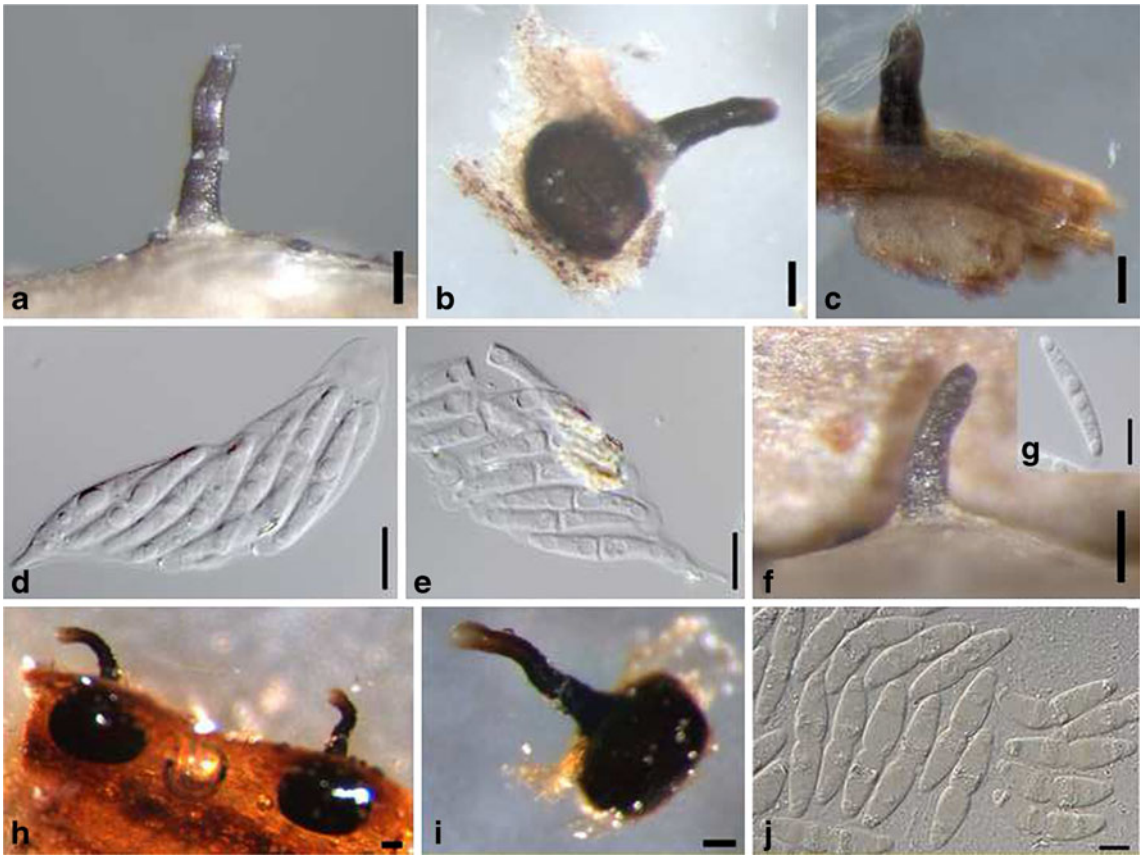

Fig. 28 *Ophiognomonia micromegala*. **a**–**b**, **d**–**g**. BPI 877612; **c**. BPI 877614; **h**– **j**. Isotype Ellis and Everhart 2309. Scale bars of perithecia= 100 μm. Scale bars of asci and ascospores=10 μm

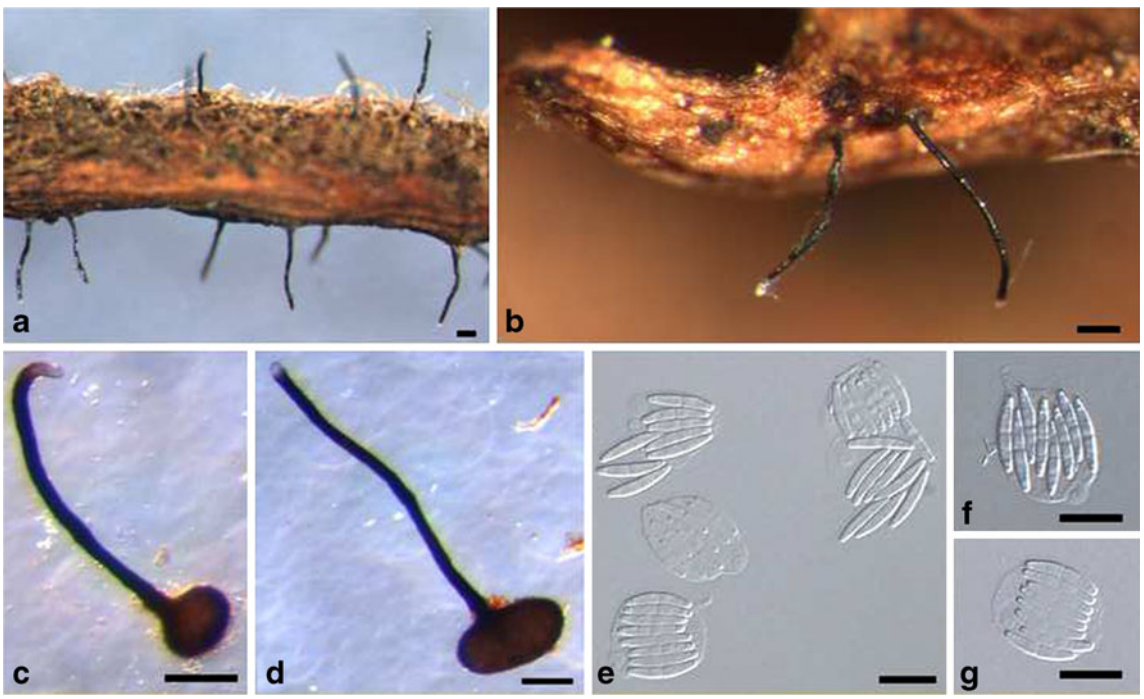

Fig. 29 *Ophiognomonia monticola*. **a**–**g**. BPI 882243. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

n2=5). Necks central to marginal, straight, curved, or sinuate, (385–)390–595(–665) μm long (mean=481, S.D. 81.5, *n*=16). Asci fusiform to ellipsoid, apex rounded, stipe acute or long tapering, apical ring conspicuous, (19–)20–22(–25)×(15–)16–17 μm (mean=22×16, S.D. 2.4, 0.9, n1=12, n2=12), ascospores arranged parallel or irregularly uniseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, slightly constricted at septum, (12–)13–14×2–3 μm (mean=13×2, S.D. 0.6, 0.4, n1=30, n2=16).

Habitat: On overwintered leaves of *Carpinus* sp. L. (Betulaceae).

Distribution: Japan (Ibaraki prefecture).

Materials examined: JAPAN, IBARAKI: Tsukuba City, west side of Mt. Tsukuba, on overwintered leaves of *Carpinus* sp., 5 April 2010, D.M. Walker (BPI 882243, culture DMW 405.3=CBS 131361).

Notes: Ophiognomonia monticola is one of 17 species known from Japan. It is one of three species worldwide known to occur on *Carpinus*, and the only species to occur on this genus in Japan.

Ophiognomonia multirostrata D.M. Walker, sp. nov. Figure 30a–g.

MycoBank: MB 564097

Etymology: multirostrata refers to the multiple necks on perithecia of this species.

Holotypus: JAPAN, IBARAKI: Tsukuba City, Tsukuba Botanical Garden, on overwintered leaves of *Alnus firma,* 6 April 2010, D.M. Walker (BPI 882226, ex-type culture DMW 364.3=CBS 131348).

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf blades, petioles, and veins, hypophyllus and epiphyllous, solitary, glossy black, subglobose, (143–)228–260(–285) μm high×(195–)299–408(–501) μm diam (mean=232×358, S.D. 54, 103, n1=5, n2=6). Necks central, straight, curved, sinuous or up to six necks per base, (752–)789–1,066(–1,203) μm long (mean=920, S.D. 114, *n*=18). Asci ellipsoid or fusiform, apex rounded, stipe acute to long tapering, (25–)26–39(–44)×(14–)15–17(–18) μm (mean=32×16, S.D. 3.9, 1.3, n1=30, n2=26), ascospores arranged uniseriate to irregularly multiseriate. Ascospores fusiform, ends rounded, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, not constricted at septum, each cell with 0–2 distinct and several small guttules, (11–)12–14(–15)×2–3 μm (mean=13×3, S.D. 1.1, 0.5, n1=30, n2=15).

Habitat: On overwintered leaves of *Alnus firma* Siebold & Zucc. (Betulaceae).

Distribution: Japan (Ibaraki prefecture).

Materials examined: JAPAN, IBARAKI: Ushiku, Ushiku Nature Reserve, on overwintered leaves of *Alnus firma,* 9 April 2010, D.M. Walker (BPI 882228, culture DMW 373.1=CBS 131400); IBARAKI: Ushiku, Ushiku Nature Reserve, on overwintered leaves of *Alnus firma,* 9 April 2010, D.M. Walker (BPI 882248, culture DMW423.1=CBS 131406).

Notes: *Ophiognomonia multirostrata* is one of 17 species known from Japan, and one of four occurring on *Alnus* from that country. Multiple-necked perithecia were occasionally observed in *O. michiganensis* and *O. multirostrata,* a phenomenon often occurring in culture, but rarely in nature for species of *Ophiognomonia*. *Ophiognomonia multirostrata* has slightly smaller ascospores than *O. naganoensis* and ascospores that overlap in size with *O. ibarakiensis,* which also occurs on *Alnus* from Japan.

Ophiognomonia naganoensis D.M. Walker, sp. nov. Figure 31a–f.

MycoBank: MB 564098

Etymology: naganoensis refers to the Japanese prefecture where the holotype was collected.

Holotypus: JAPAN, NAGANO: Ueda-shi, Sugadaira, waterfall at the Sugadaira Montane Research Center, on overwintered leaves of *Alnus hirsuta,* 13 April 2010, D.M. Walker (BPI 882246, ex-type culture DMW 418.3=CBS 131404).

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf blades and veins, hypophyllous and epiphyllous, solitary to aggregated up to two, glossy black, subglobose, (351–)372–386(–391) μm high×(432–)456–523(–565) μm diam (mean=376×494, S.D. 18.8, 61, n1=4, n2=4). Necks central, straight, curved, or sinuous, (434–)491–913(–917) μm long (mean=683, S.D. 127.5, *n*=17). Asci ellipsoid to fusiform, apex rounded, stipe acute, rounded, or long tapering, apical ring conspicuous, (32–)33–47(–48)×(8–)9–20(–21) μm (mean=38×16, S.D. 5.5, 4.5, n1=30, n2=30), ascospores arranged uniseriate to irregularly multiseriate. Ascospores fusiform, rounded ends, straight to slightly curved, one-septate, median to

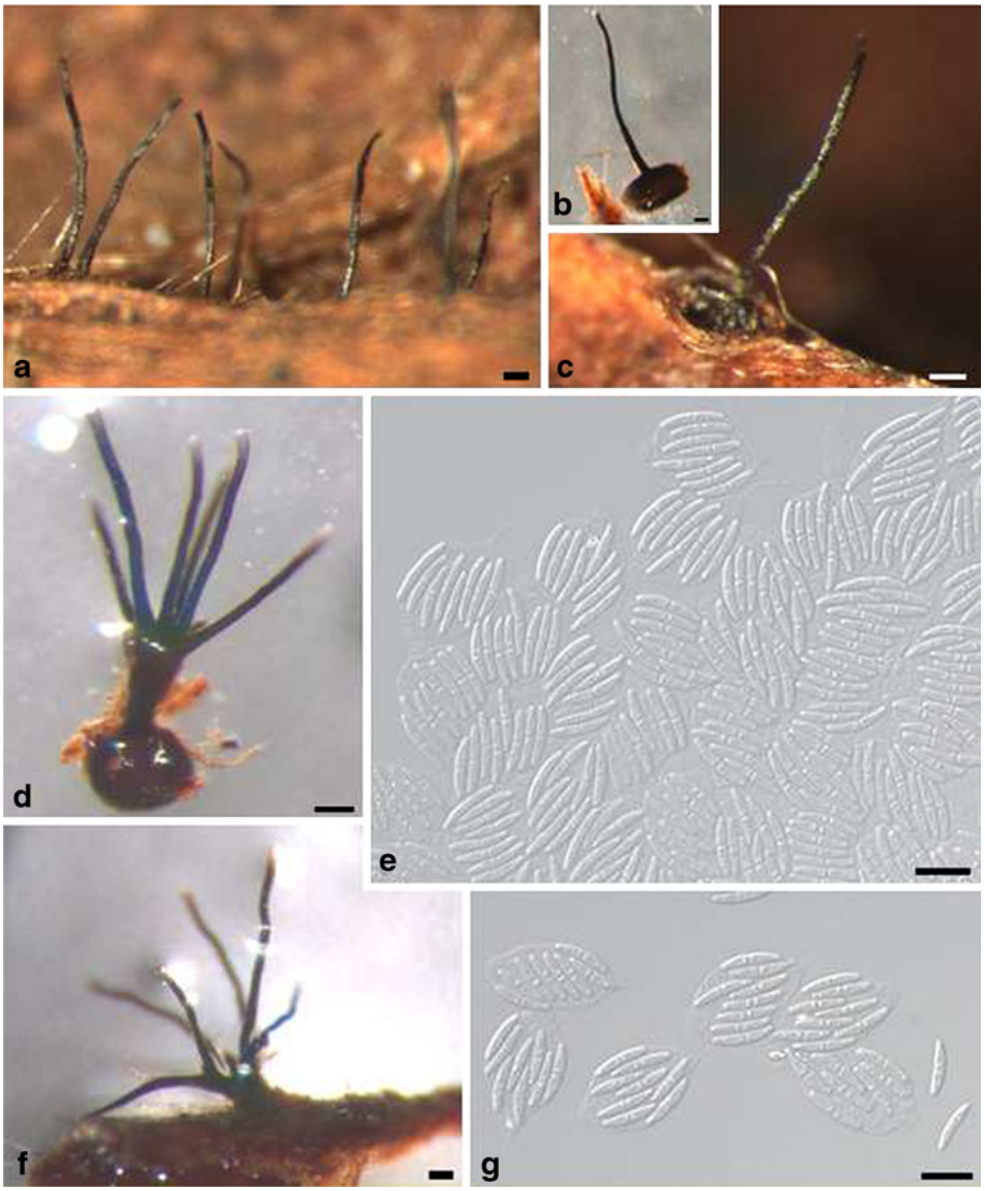

Fig. 30 *Ophiognomonia multirostrata*. **d**–**f**. BPI 882248; **b**–**c**. Holotype BPI 882226; **a**, **g**. BPI 882228. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

indistinctly sub- or supramedian, slightly constricted at septum, each cell with 0–2 distinct guttules and several small guttules, (18–)19–20(–21)×3–4 μm (mean=19×4, S.D. 0.8, 0.5, n1=30, n2=15).

Habitat: On overwintered leaves of *Alnus hirsuta* Turcz. and *A. hirsuta* Turcz. *f. sibirica* (Spach) H. Ohba (Betulaceae).

Distribution: Japan (Nagano prefecture).

Materials examined: JAPAN, NAGANO: Ueda-shi, Sugadaira, waterfall at the Sugadaira Montane Research Center, on overwintered leaves of *Alnus hirsuta* var. *sibirica,* 6 April 2010, D.M. Walker (BPI 882244, culture DMW 410.1=CBS 131362); NAGANO: Ueda-shi, Sugadaira, waterfall at the Sugadaira Montane Research Center, on overwintered leaves of *Alnus hirsuta* var. *sibirica,* 13 April 2010, D.M. Walker (BPI 882211, culture DMW 331.2=CBS 131338).

Notes: *Ophiognomonia naganoensis* is one of 17 species known from Japan, and one of four occurring on *Alnus* from that country. This species has slightly larger ascospores than *O. multirostrata* and *O. ibarakiensis,* which also occur on *Alnus* in Japan.

Ophiognomonia nana (Rehm) Sogonov, Stud. Mycol. 62: 63. 2008. Figure 32a–f.

Basionym: *Gnomoniella nana* Rehm, Hedwigia 42: 349. 1903.

MycoBank: MB 512189

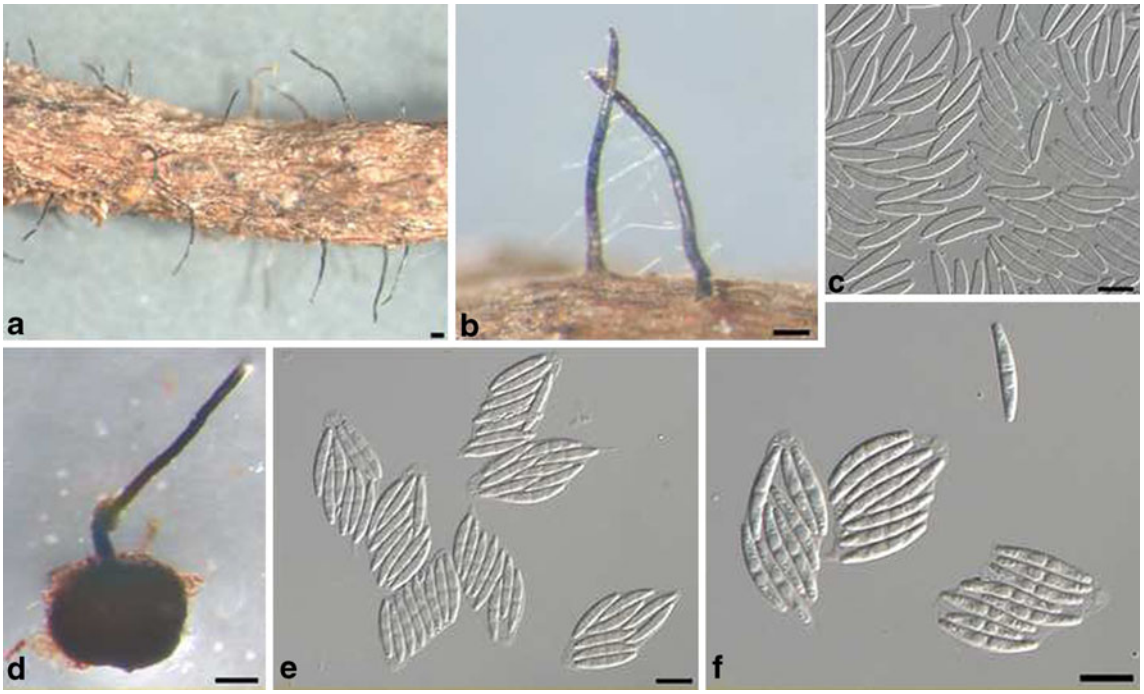

Fig. 31 *Ophiognomonia naganoensis*. **a**–**b**. Holotype BPI 882246; **c**, **e**–**f**. BPI 882244; **d**. BPI 882211. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Perithecia immersed to partially erumpent, causing host tissue to swell, on leaf blades and veins, epiphyllous and hypophyllous, solitary, glossy black, subglobose, 287 μm high×347 μm diam (n1=1, n2=1). Necks central, straight to curved, 808–841 μm long (mean=824, S.D. 23, *n*=2). Asci obovoid to pyriform, apex papillate, stipe acute to long tapering, apical ring conspicuous, (42–)45–49(–60)×(21–)25–26(–27) μm (mean=48×25, S.D. 7, 2.5, n1=5, n2=5), ascospores arranged irregularly multiseriate. Ascospores lenticular with acute to rounded ends, single celled, non-

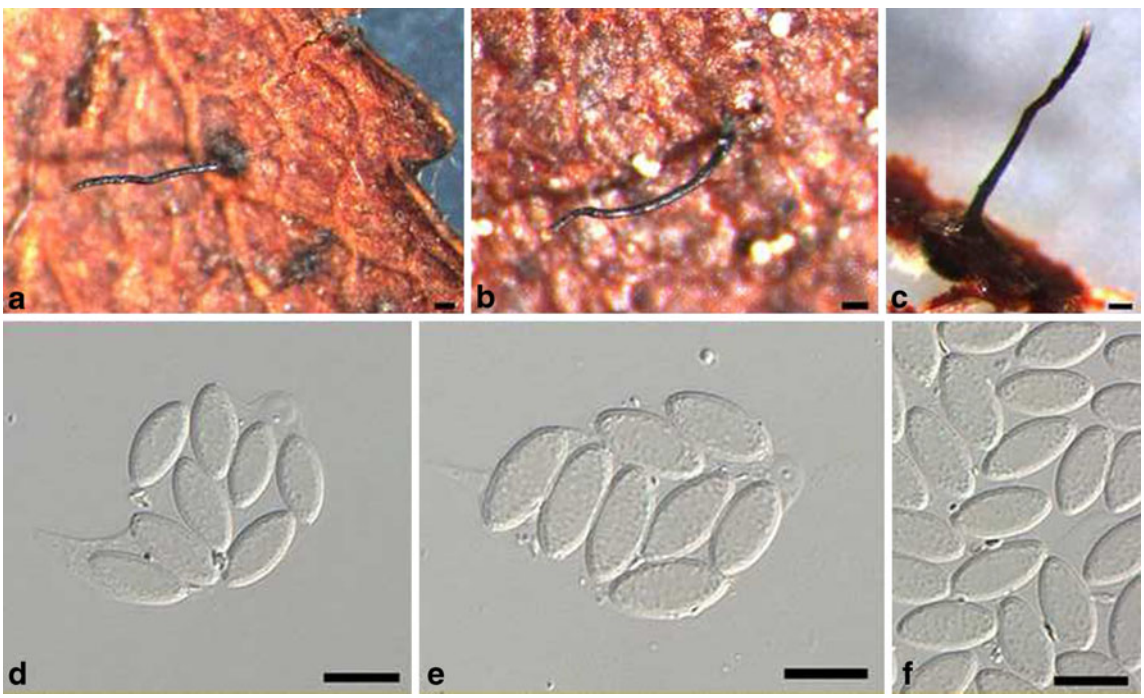

Fig. 32 *Ophiognomonia nana*. **a**–**f**. Lectotype Rehm Ascomyceten 1522. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

septate, lacking guttules, (12–)13–15(–16)×6–7 μm (mean=14×6, S.D. 1, 0.5, n1=30, n2=23).

Habitat: On leaves of *Betula nana* L. (Betulaceae).

Distribution: Europe (Germany).

Materials examined: GERMANY: Oberbayern, Bernried, on leaves of *Betula nana,* May 1903, Rehm (Rehm Ascomyceten 1522, LECTOTYPE of *Gnomoniella nana* designated here, FH).

Notes: This is the only species of *Ophiognomonia* with single celled, non-septate ascospores. Seven species of *Ophiognomonia* including *O. nana* occur on the genus *Betula* having a global temperate distribution.

Ophiognomonia nipponicae D.M. Walker, sp. nov. Figure 33a–i.

MycoBank: MB 564099

Etymology: nipponicae refers to the host plant epithet on which the holotype was collected.

Holotypus: JAPAN, IBARAKI: Tsukuba City, hiking trail around Mt. Tsukuba shrine, on overwintered leaves of *Prunus nipponica,* 6 April 2010, D.M. Walker (BPI 882249, ex-type culture DMW 424.1=CBS 131407).

Perithecia immersed, on leaf blades and veins, solitary or in dense clusters, glossy black, globose to subglobose, (201–)244–298(–316) μm high×(–227)261–306 (–422) μm diam (mean=265×302, S.D. 45.4, 73.8, n1=5, n2=5). Necks central to marginal, curved, sinuous, or straight, (965–)968–1,385(–1,403) μm long (mean=1,153, S.D. 126.7, *n*=15). Asci fusiform to ellipsoid, apex papillate or rounded, stipe tapering, (34–)35–46(–48)×(13–)14–15(–16) μm (mean=38×15, S.D. 3.8, 0.8, n1=22, n2=21), ascospores arranged parallel or irregularly uniseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, not constricted at septum, with appendages short, corniform to subulate or absent, (15–)16–17(–18)×2 μm (mean=17×2, S.D. 3.2, 0.0, n1=30, n2=23).

Habitat: On overwinterd leaves of *Prunus nipponica* Matsum. (Rosaceae).

Distribution: Japan (Ibaraki prefecture).

Notes: Ophiognomonia nipponicae is one of 17 species known from Japan, and one of two species occuring on *Prunus* from that country. This species has longer perithecial necks and larger ascospores than *O. japonica,* which also occurs on *Prunus* in Japan. Ascospore appendages were observed in *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.*

Ophiognomonia ostryae-virginianae D.M. Walker & L.C. Mejía, sp. nov. Figure 34a–f.

MycoBank: MB 564100

Etymology: ostryae-virginianae refers to the host *Ostrya virginiana* from which the holotype was collected.

Holotypus: UNITED STATES, NEW YORK: Tompkins County, Ithaca, Buttermilk Falls State Park, on overwintered leaves of *Ostrya virginiana,* 7 June 2007, L.C. Mejía, det. D.M. Walker (BPI 879596, ex-type culture LCM 155.01=CBS 131398).

Perithecia immersed, occasionally causing host tissue to swell, on leaf blades and veins, hypophyllous and epiphyllous, solitary, glossy black, globose to subglobose, (136–)146–166(–179) μm high×(164–)166–168(–200) μm diam (mean=157×175, S.D. 19, 17, n1=4, n2=4). Necks central, straight to curved, (236–)325–432(–438) μm long (mean=361, S.D. 74, *n*=7). Asci ellipsoid to fusiform, apex papillate or rounded, stipe acute, rounded or tapering, apical ring conspicuous, (26–)27–40(–43)×(13–)14–16(–17) μm (mean=32×15, S.D. 5.3, 1, n1=17, n2=17), ascospores arranged parallel to irregularly uniseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median, slightly to not constricted at septum, each cell with 0–2 distinct and several small guttules, (13–)14–15(–16)×2–3 μm (mean=14×2, S.D. 0.8, 0.5, n1=29, n2=21).

Habitat: On overwintered leaves of *Ostrya virginiana* K. Koch (Betulaceae).

Distribution: United States (NY).

Notes: This is the only species known to occur on *Ostrya* in the Betulaceae and may represent a novel host shift to this genus.

Ophiognomonia otanii D.M. Walker, sp. nov. Figure 35a–h.

MycoBank: MB 564101

Etymology: otanii was named after Yoshio Otani to honor his contribution to the taxonomy of the Diaporthales of Japan.

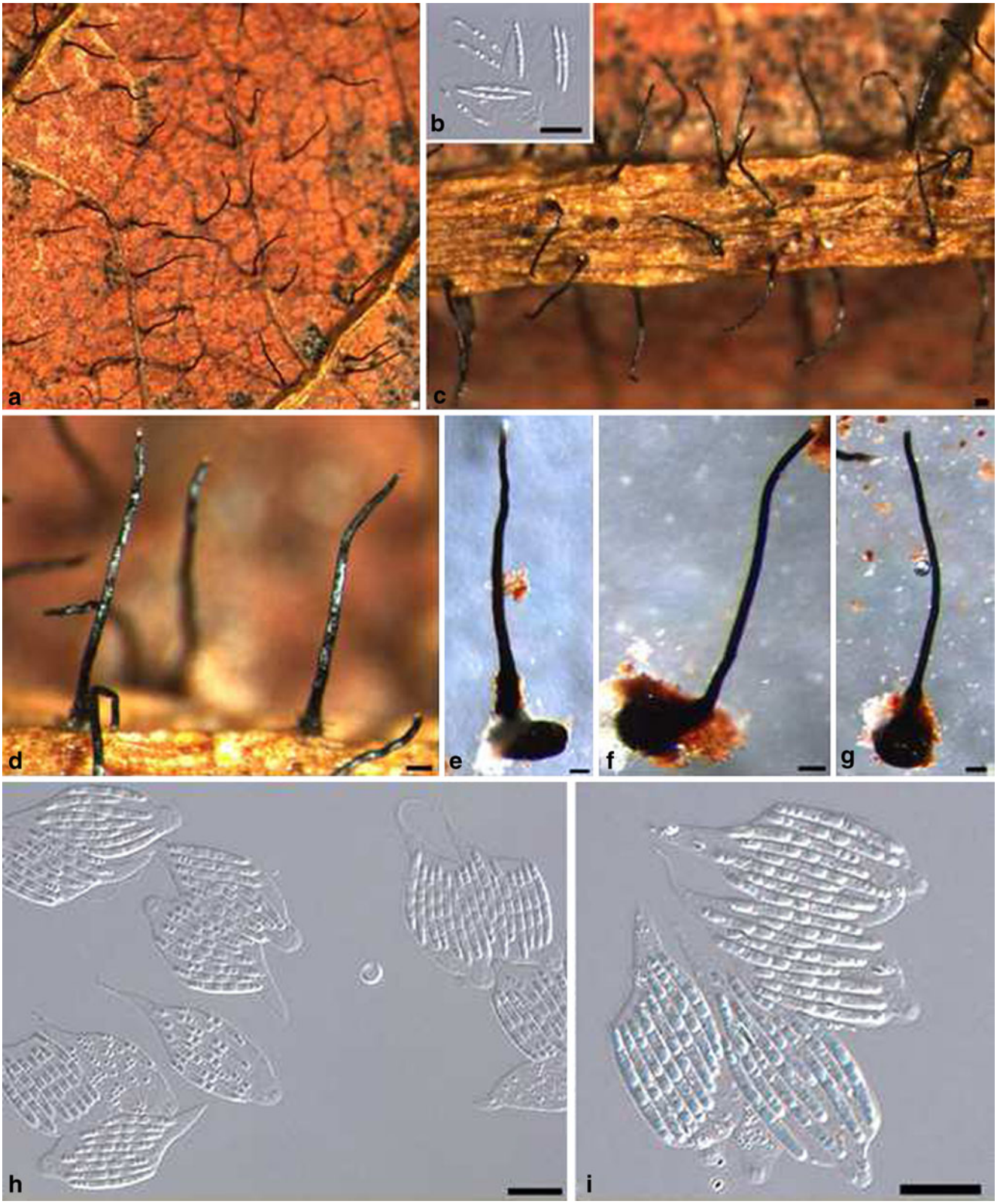

Fig. 33 *Ophiognomonia nipponicae*. **a**–**i**. Holotype BPI 882249. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Holotypus: JAPAN, NAGANO: Ueda-shi, Sugadaira, Kakuma River Trail, on overwintered leaves of *Castanea crenata,* 14 April 2010, D.M. Walker (BPI 882234, ex-type culture DMW385.1=CBS 131354).

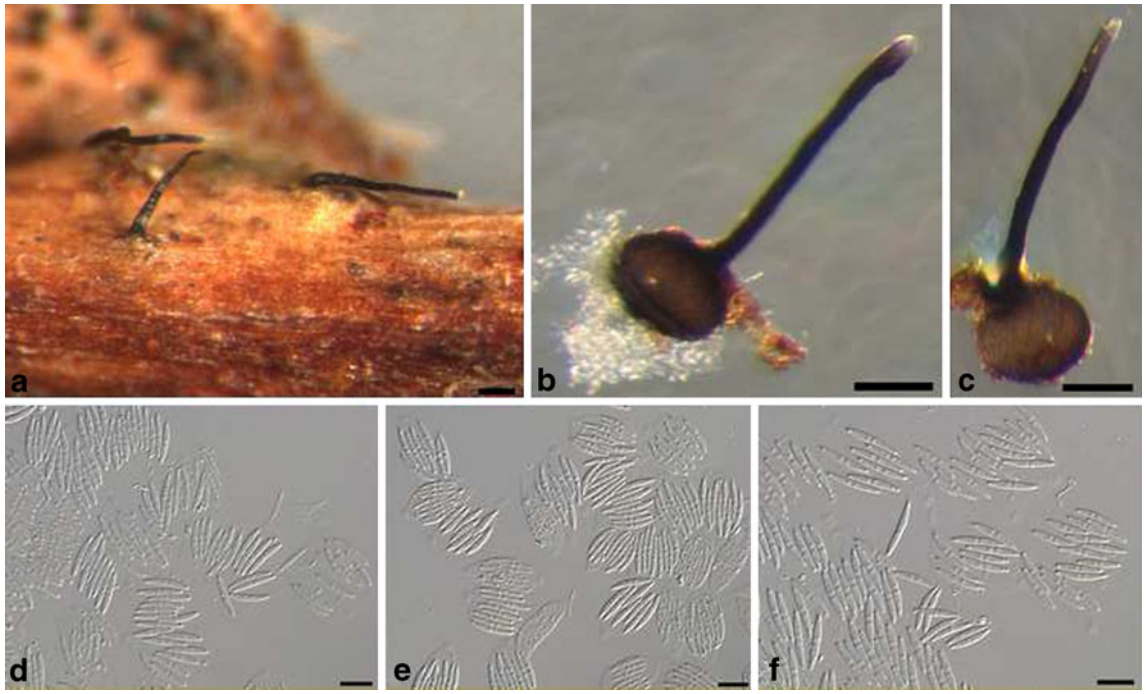

Fig. 34 *Ophiognomonia ostryae-virginianae*. **a**–**f**. Holotype BPI 879596. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf petioles, veins, and blades, solitary or aggregated up to two, glossy black, subglobose, (165–)175–323(–330) high×(220–)226–387(–406) μm diam (mean=242×310, S.D. 54, 62, n1=11, n2=11). Necks central to marginal, straight to curved, (482–)508–1,032(–1,174) μm long (mean=746, S.D. 171.6, *n*=30). Asci fusiform to ellipsoid, apex papillate or rounded, stipe tapering or occasionally papillate to rounded, apical ring conspicuous (24–)25–33(–34)×(13–)14–16(–17) μm

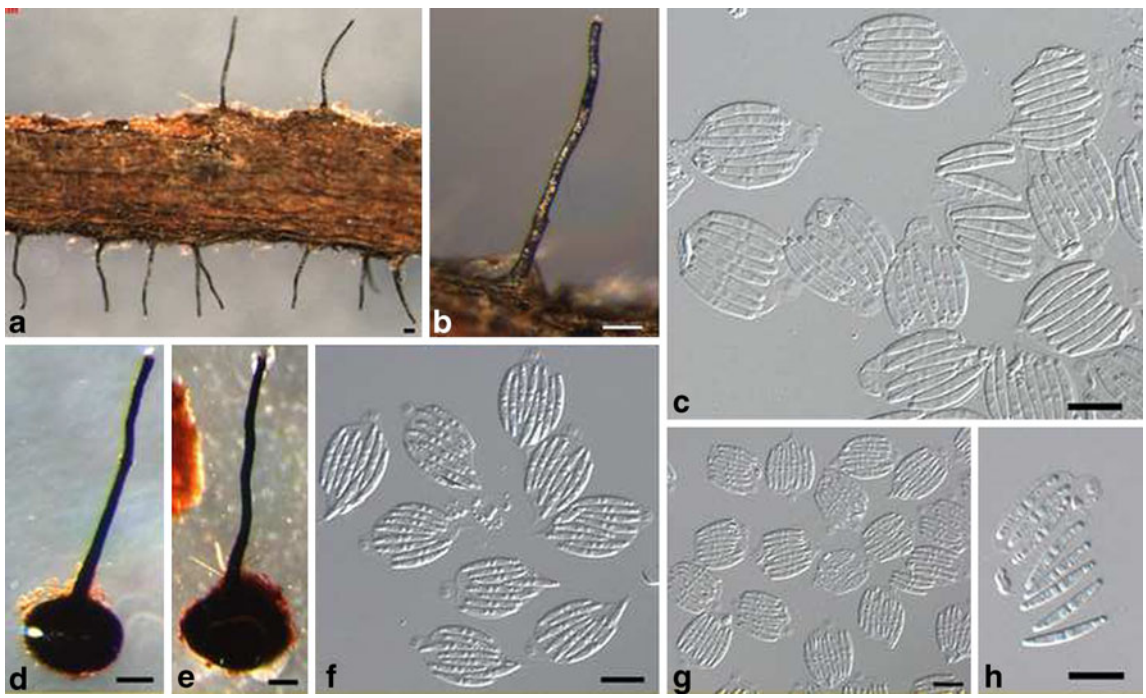

Fig. 35 *Ophiognomonia otanii*. **a**–**b**. Holotype BPI 882234; **e**–**f**, **h**. BPI 882237; **c**–**d**, **g**. BPI 882241. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

(mean=28×16, S.D. 2.6, 1.1, n1=26, n2=27), ascospores arranged parallel or irregularly uniseriate. Ascospores fusiform with rounded ends, mostly straight, rarely slightly curved, one-septate, indistinctly submedian, not constricted at septum, each cell with 0–2 distinct and several small guttules, 14–15(–16)×2–3 μm (mean=15×2, S.D. 0.7, 0.4, n1=30, n2=30).

Habitat: On overwintered leaves of *Castanea crenata* Siebold & Zucc. (Fagaceae).

Distribution: Japan (Gunma, Ibaraki, and Nagano prefectures).

Materials examined: JAPAN, GUNMA: Azuma, Azuma Forest Park, on overwintered leaves of *Castanea crenata,* 12 April 2010, D.M. Walker (BPI 882237, culture DMW 390.1=CBS 131356); IBARAKI: Ushiku Nature Reserve, on overwintered leaves of *Castanea crenata,* 9 April 2010, D.M. Walker (BPI 882242, culture DMW 401.3=CBS 131402); NAGANO: Ueda-shi, Sugadaira, Kakuma River Trail, on overwintered leaves of *Castanea crenata,* 14 April 2010, D.M. Walker (BPI 882241, culture DMW 397.1=CBS 131360).

Notes: *Ophiognomonia otanii* is one of 17 species known from Japan and one of three occuring on *Castanea* in that country. A distinct submedian septum was observed in ascospores of four species including *O. alni-cordatae, O. apiospora, O. gei-montani,* and *O. otanii.* A group of closely related species including *O. asiatica, O. kobayashii, O. otanii,* and *O. sogonovii* are specific to *Quercus* spp. and *Castanea* spp. within the Fagaceae (Fig. 2).

Ophiognomonia padicola (Lib.) M. Monod, Beih. Sydowia 9: 158. 1983.

Basionym: *Sphaeria padicola* Lib., Plant. Cryptog. Arduenn. Cent. 2: 149. 1832.
≡ *Gnomonia padicola* (Lib.) Kleb., Z. Pflkrankh. 18: 137. 1908.
=*Ophiognomonia padi* Jaap, Verh. bot. Ver. Prov. Brandenburg 47: 87. 1905 *fide* Monod 1983.

Habitat: On overwintered leaves of *Prunus padus* L. (Rosaceae).

Distribution: Europe (Germany, Switzerland).

Notes: This is the only species of *Ophiognomonia* known to occur on *Prunus* from Europe. For a detailed description of this species, see Monod (1983).

Ophiognomonia pseudoclavulata Sogonov, Stud. Mycol. 62: 51. 2008. Figure 36a–g.

Habitat: On overwintered leaves of *Carya* sp. Nutt. *Carya tomentosa* (Lam.) Nutt. (Juglandaceae).

Distribution: United States (DC, IL, IN, MD, NC, NJ, PA, TN, VA).

Materials examined: UNITED STATES, MARYLAND: Frederick and Carroll Counties, Patapsco State Park, on overwintered leaves of *Carya* sp., 11 April 2011, D.M. Walker (BPI 882283, culture DMW 538=CBS 131434); MARYLAND: Prince George's County, Beltsville Agricultural Research Center, on overwintered leaves of *Carya* sp., 28 April 2011, D.M. Walker (BPI 882290, culture DMW 551=CBS 131367); PENNSYLVANIA: Kennett Square County, vicinity of Philadelphia, near Phillips mushroom farm, *Carya tomentosa,* 17 April 2004, M.V. Sogonov (HOLOTYPE, BPI 844280, ex-type culture AR4059=CBS 121236).

Notes: Ophiognomonia lenticulispora and *O. pseudoclavulata* are the only species of *Ophiognomonia* with oval to ellipsoid ascospores. In addition, ascospore appendages were observed in *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata, O. pseudoischnostyla,* and *O. setacea.* For a detailed description of this species, see Sogonov et al. (2008).

Ophiognomonia pseudoischnostyla, D.M. Walker, sp. nov. Figure 37a–f.

Mycobank: MB 564102

Etymology: pseudoischnostyla refers to the resemblance to *O. ischnostyla.*

Holotypus: RUSSIA, TVER' PROVINCE: Toropets district, vicinity of v. Bubonitsy, biological research station Chisty Les, on leaves of *Betula verrucosa,* 31 August 2004, M.V. Sogonov (BPI 877616, ex-type culture CBS 121228).

Perithecia immersed, occasionally causing host tissue to swell, on leaf petioles and veins, hypophyllous to epiphyllous, solitary or aggregated up to two, glossy black, globose to subglobose, (205–)222–272(–316) μm high×(227–)280–397(–537) μm diam (mean=248×335, S.D. 38, 96, n1=8, n2=8). Necks central to marginal, mostly straight or curved to sinuous, occasionally swollen at the tip, (509–)557–890(–902) μm long (mean=684, S.D. 117.8, *n*=15). Asci fusiform, apex rounded, acute stipe, apical ring conspicuous, (33–)34–47(–48)×(14–)16–17 μm (mean=40×16, S.D. 6.3, 1.1, n1=8, n2=8), ascospores arranged parallel or irregularly uniseriate, fusiform, ends rounded, straight to slightly curved, one-septate, median to indistinctly

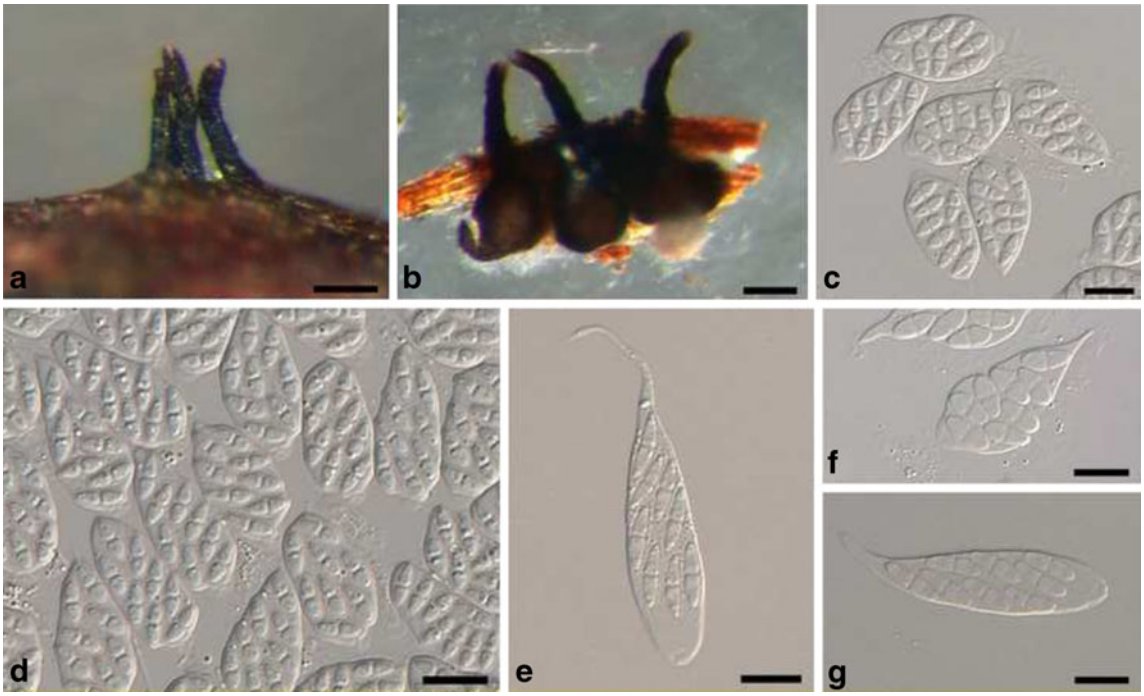

Fig. 36 *Ophiognomonia pseudoclavulata*. **a**–**b**, **e**, **g**. BPI 882283; **c**–**d**, **f**. BPI 882290. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

sub- or supramedian, slight constriction at septum, appendages subulate to whip-shaped or absent, (13–)14–19(–20)× 2–3 μm (mean=17×2, S.D. 2.1, 0.5, n1=30, n2=28).

Habitat: On overwintered leaves of *Alnus glutinosa* (L.) Gaertn., *A. incana* (L.) Moench, and *Betula pubescens* Ehrh. (Betulaceae).

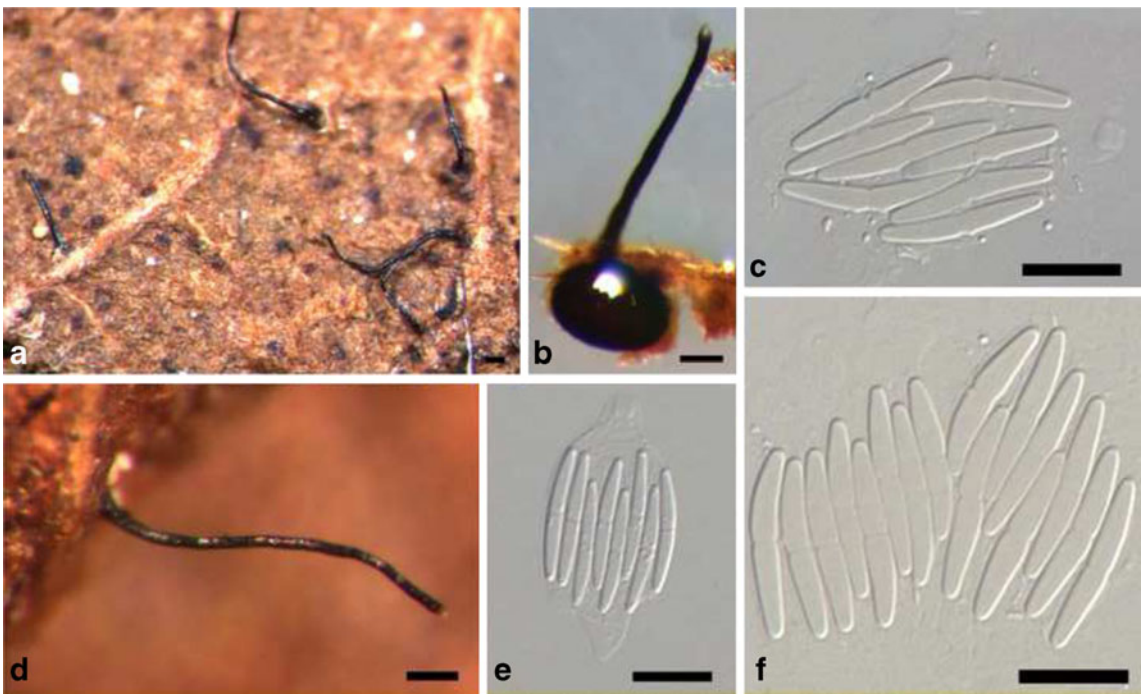

Fig. 37 *Ophiognomonia pseudoischnostyla.* **a**, **c**–**d**, **f**. BPI 877617; **b**, **e**. BPI 877619. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Distribution: Europe (Switzerland) and Russia (Novogorod and Tver' provinces).

Materials examined: RUSSIA, NOVOGOROD PROVINCE: Kholm district, Rdeysky Natural Reserve, vicinity of village Fryunino, on overwintered leaves of *Alnus glutinosa,* 11 June 2005, M.V. Sogonov (BPI 877619, GenBank EU 294900); TVER' PROVINCE: Toropets district, v. Kosilovo, on overwintered leaves of *Alnus glutinosa,* 5 June 2005, M.V. Sogonov (BPI 877617, EU 254907); TVER' PROVINCE: Toropets district, vicinity of v. Bubonitsy, biological research station Chisty Les, leaves of *Alnus glutinosa,* 14 June 2005, M.V. Sogonov (BPI 877618, GenBank EU 254908). SWITZERLAND: Wallis, Mörel, on overwintered leaves of *Alnus incana,* 28 May 2005, M.V. Sogonov (BPI 877620, GenBank EU 254898).

Notes: This species is morphologically similar to *O. ischnostyla,* however, *O. ischnostyla* occurs on *Carpinus* spp. and *Corylus* spp., whereas *O. pseudoischnostyla* occurs on *Alnus* spp. and *Betula* spp. Ascospore appendages were observed in this species and *O. balsamiferae, O. gei, O. hiawathae, O. intermedia, O. ischnostyla, O. longispora, O. melanostyla, O. michiganensis, O. nipponicae, O. pseudoclavulata,* and *O. setacea.*

Ophiognomonia pterocaryae D.M. Walker, sp. nov. Figure 38a–f.

MycoBank: MB 564103

Etymology: pterocaryae refers to the host genus on which the holotype was collected.

Holotypus: JAPAN, NAGANO: Ueda-shi, Sugadaira, Kakuma River Trail, on overwintered leaves of *Pterocarya rhoifolia,* 14 April 2010, D.M. Walker (BPI 882240, ex-type culture DMW 396.3=CBS 131359).

Perithecia immersed to erumpent, occasionally causing host tissue to swell, on leaf blades, veins, petioles, and rachises, hypophyllous, solitary, loosely aggregated, or clusters up to three, glossy black, subglobose, (206–)212–312(–313) μm high×(287–)307–423(–424) μm diam (mean=274×353, S.D. 41.6, 49.7, n1=9, n2=9). Necks central, marginal, or lateral, straight to curved, (351–)400–646(–726) μm long (mean=533, S.D. 107.5, *n*=13). Asci clavate to fusiform, apex rounded to papillate, stipe acute to long tapering, (38–)39–59(–68)×(15–)16–17(–18) μm (mean=47×17, S.D. 8.5, 1.1, n1=16, n2=16), ascospores arranged uniseriate to irregularly multiseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, not constricted at septum, (14–)15–18(–19)×3–4 μm (mean=17×3, S.D. 1.1, 0.3, n1=30, n2=27).

Habitat: On overwintered leaves of *Pterocarya rhoifolia* Siebold & Zucc. (Juglandaceae).

Distribution: Japan (Nagano prefecture).

Materials examined: JAPAN, NAGANO: Ueda-shi, Sugadaira, Kakuma River Trail, on overwintered leaves of *Pterocarya rhoifolia,* 14 April 2010, D.M. Walker (BPI 882219, culture DMW 350.2=CBS 131344).

Notes: *Ophiognomonia pterocaryae* is one of 17 species known from Japan, and one of two known to occur on *Pterocarya* from that country. Of the species on *Pterocarya, O. cordicarpa* has long filiform ascospores, whereas *O. pterocaryae* has much shorter fusiform ascospores. Several other species are known to occur on *Carya* and *Juglans* in the Juglandaceae, including the pathogens *O. leptostyla* and *O. clavigignenti-juglandacearum.*

Ophiognomonia quercus-gambellii (M. Monod) D.M. Walker, comb. nov. Figure 39a–h.

Basionym: *Gnomonia quercus-gambellii* M. Monod, Beih. Sydowia 9: 98. 1983.

MycoBank: MB 564104

Perithecia immersed, causing host tissue to swell, rupture, and expose bases, on leaf blades and veins, hypophyllous, solitary, glossy black, globose to subglobose, (142–)163–209(–229) μm high×(157–)178–255(–268) μm diam (mean=192×221, S.D. 29, 36, n1=10, n2=10). Necks central, rarely two necks per base, upright, straight to curved or sinuous, tips often swollen, (229–)331–439(–480) μm long (mean=310, S.D. 85, *n*=13). Asci fusiform to obovoid with rounded apex and stipe, apical ring sometimes conspicuous, (29–)30–44(–46)×(10–)11–15(–16) μm (mean=38×12, S.D. 4.7, 1.8, n1=21, n2=21), ascospores arranged obliquely uniseriate to irregularly multiseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to submedian or supramedian, not constricted or slightly constricted at septum, each cell with several small guttules, (11–)12–14(–15)×(2–)3–4 μm (mean=13×3, S.D. 0.9, 0.6, n1=30, n2=30).

Habitat: On overwintered leaves of *Quercus gambellii* Liebm. and *Q. kelloggii* Newberry (Fagaceae).

Distribution: United States (AZ, OR).

Materials examined: UNITED STATES, ARIZONA: Coconino County, North Rim of the Grand Canyon, leaves

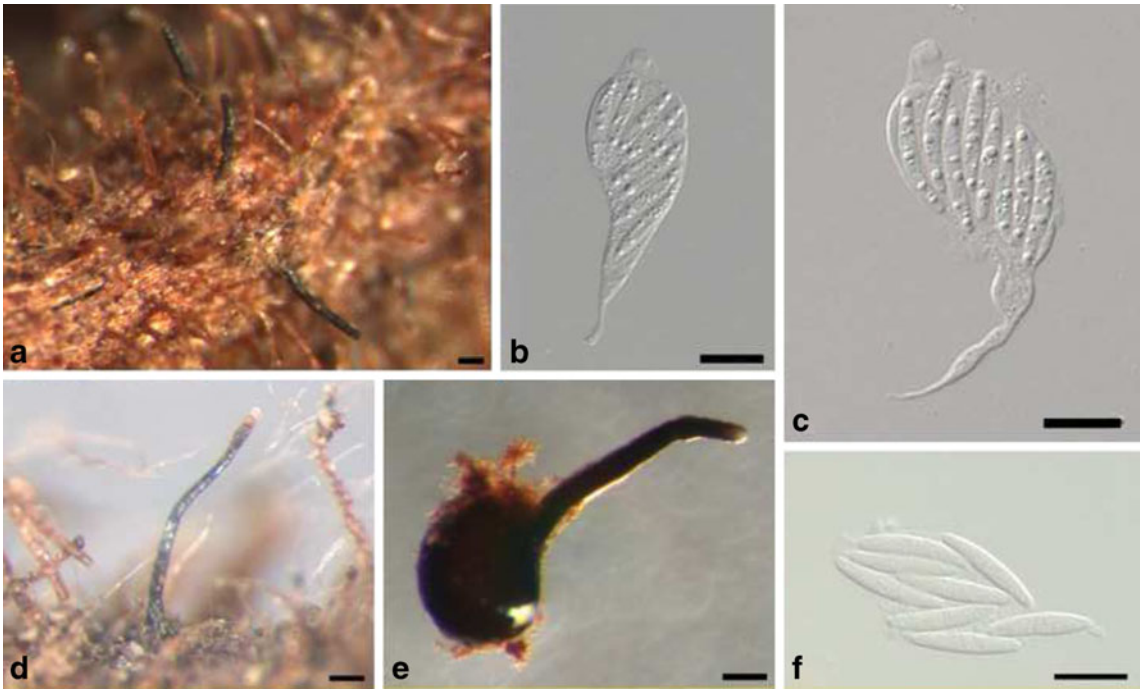

Fig. 38 *Ophiognomonia pterocaryae*. **a**–**c**, **e**. BPI 882219; **d**, **f**. Holotype BPI 882240. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

of *Quercus gambellii,* 18 August 1973, M.E. Barr (Barr 6095 collected as *Gnomonia fasciculata*, HOLOTYPE of *Gnomonia quercus-gambellii,* NY); OREGON: Jackson County, McGregor and Casey Park, on overwintered leaves of *Quercus kelloggii,* 20 May 2010, D.M. Walker (BPI 882202, EPITYPE designated here, ex-epitype culture DMW 117.1=CBS 131397).

Notes: Ophiognomonia quercus-gambellii, based on *Gnomonia quercus-gambellii*, was originally collected by M.E. Barr in

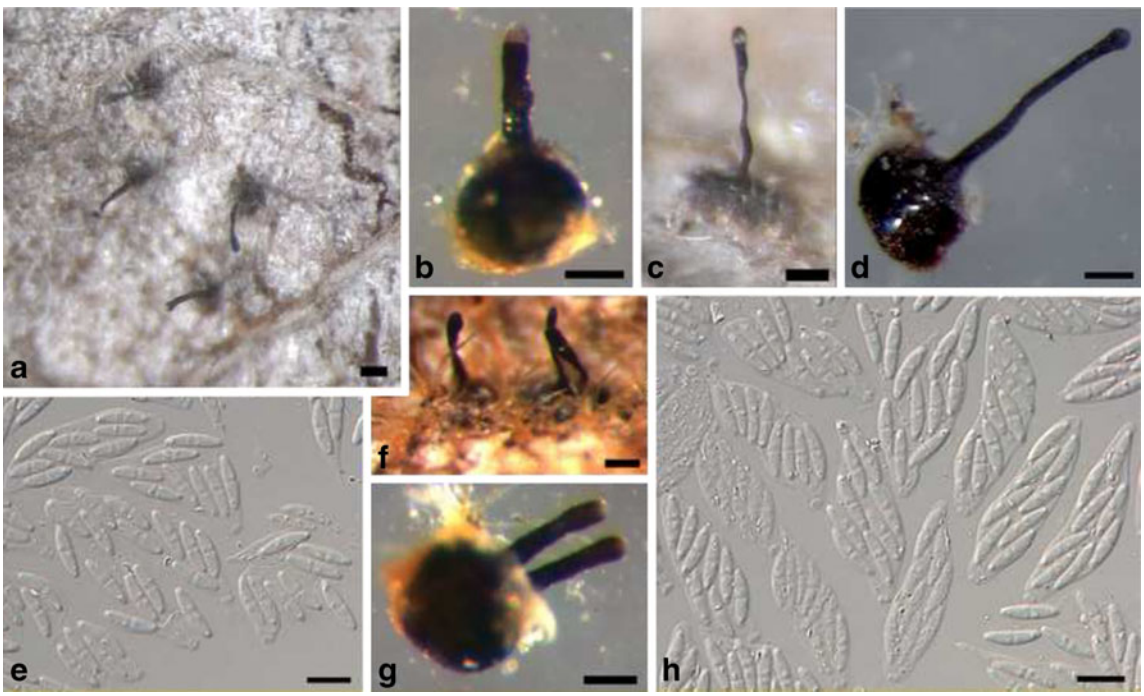

Fig. 39 *Ophiognomonia quercus-gambellii*. **a**, **c**, **d**. Epitype BPI 882202; **b**, **e**–**h**. Holotype Barr 6095. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Arizona, U.S.A. who identified this specimen as *Gnomonia fasciculata* Fuckel (Barr 1978). A specimen was collected and culture obtained (BPI 882202=CBS 131397) on *Quercus kellogii* from Oregon, U.S.A. that is morphologically identical to the type specimen of *G. quercus-gambellii* (Barr 6095). The Oregon specimen is designated as the epitype. Both *O. quercus-gambellii* and *G. fasciculata* occur on *Quercus* spp. *Ophiognomonia quercus-gambellii* is one of four species of *Ophiognomonia* known to occur exclusively on *Quercus.*

Ophiognomonia rosae (Fuckel) Kirschst., Annls mycol. 37 (1/2): 129. 1939. Figure 40a–h.

Basionym: *Gnomonia rosae* Fuckel, Jb. nassau. Ver. Naturk. 23–24: 122. 1870.

≡ *Gnomoniella rosae* (Fuckel) Sacc., Syll. Fung. 1: 416. 1882.

MycoBank: MB 276702

Perithecia immersed, occasionally causing host tissue to swell, on leaf blades and veins, hypophyllous, solitary, glossy black, subglobose, (249–)296–312(–336) μm high× (247–)300–389(–442) μm diam (mean=298×338, S.D. 32, 77, n1=5, n2=5). Necks central, straight to curved, (245–)430–1,451(–1,784) μm long (mean=611, S.D. 223.1, *n*=10). Asci fusiform, apex papillate or rounded, stipe long tapering, apical ring conspicuous, (26–)29–38(–40)×(11–)12–15(–16) μm (mean=34×13, S.D. 3.3, 1.3, n1=25, n2=29), ascospores arranged irregularly multiseriate or parallel. Ascospores narrowly fusiform to fusiform, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, slightly constricted at septum, each cell with 0–2 distinct guttules, (13–)14–20(–21)×(1–)2–3 μm (mean=16×2, S.D. 2.4, 0.6, n1=30, n2=30).

Habitat: On overwintered leaves of *Fragaria vesca* L., *Rosa* sp. L., and *Rubus* sp. L. (Rosaceae).

Distribution: Europe (Finland, France, Switzerland) and United States (OR).

Materials examined: FRANCE: Veronnes, leaves of *Rubus* sp., April 2011, A. Gardiennet (BPI 882286, EPITYPE designated here, ex-epitype culture DMW 543=CBS 131365); SWITZERLAND: *Rosa* sp., 1870, Fuckel, (Fuckel Fungi Rhenani 1790, LECTOTYPE of *Sphaeria rosae* designated here, FH). UNITED STATES, OREGON: Jackson County, Prospect, River Bridge campground, Upper Rouge River trailhead, on overwintered leaves of *Fragaria vesca,* D.M. Walker (BPI 882201, culture DMW 108.2=CBS 128442).

Notes: This species is one of nine that occur on hosts in the Rosaceae, and one of eight that occur on multiple genera in this host family. *Ophiognomonia rosae* has long perithecial necks relative to many other species of *Ophiognomonia.*

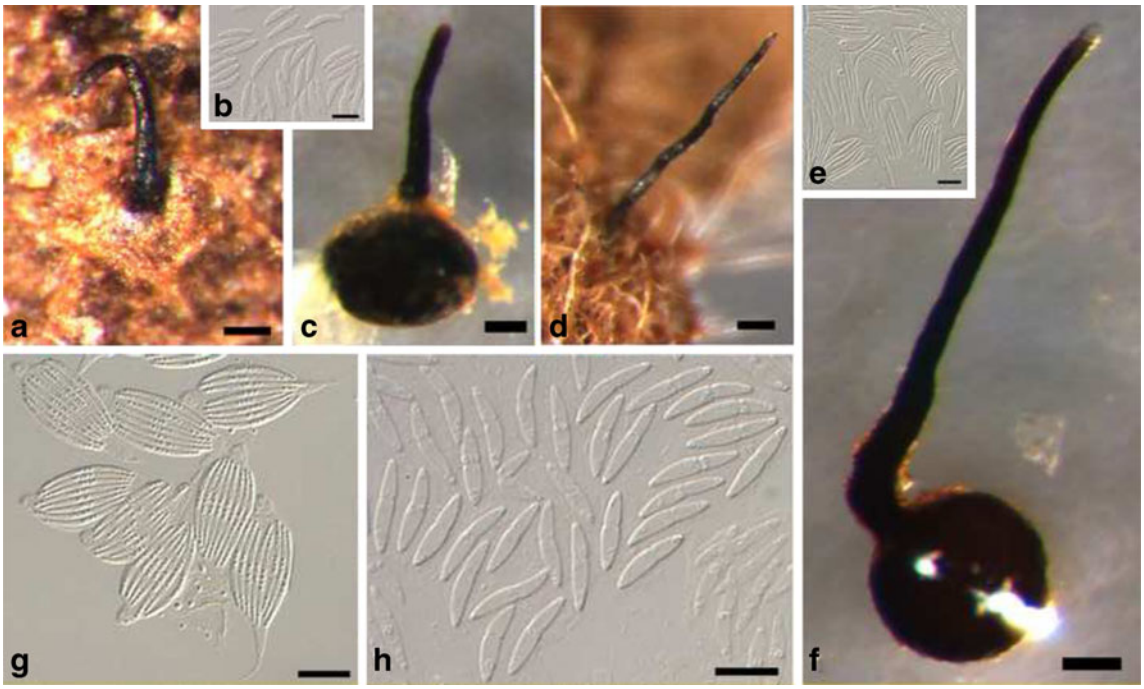

Fig. 40 *Ophiognomonia rosae*. **a**–**c**. **h**. Holotype Fuckel Fungi Rehnani 1790; **d**–**g**. Epitype BPI 882286. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

Ophiognomonia rubi-idaei (M. Monod) Sogonov, Stud. Mycol. 62: 64. 2008. Figure 41a–g.

Basionym: *Gnomonia rubi-idaei* M. Monod, Beih. Sydowia 9: 106. 1983.

MycoBank: MB 512190

Perithecia immersed, occasionally causing host tissue to swell, on leaf blades and veins, hypophyllous, solitary, glossy black, subglobose, (325–)373–520(–521) μm high×(447–)483–686 (–719) μm diam (mean=430×588, S.D. 77, 105, n1=7, n2=7). Necks central to lateral, straight to curved, (835–)883–1,973(–2,054) μm long (mean=1,460, S.D. 521, *n*=6). Asci fusiform, narrow, apex rounded or papillate, stipe long tapering, apical ring conspicuous, (27–)28–48(–49)×(7–)8–14(–17) μm (mean=38×10, S.D. 7.1, 2.6, n1=24, n2=21), ascospores arranged regularly to irregularly parallel or multiseriate. Ascospores narrowly fusiform with rounded ends, straight to slightly curved, one-septate, median to submedian, not constricted at septum, (12–)13–16(–17)×2 μm (mean=15×2, S.D. 1.1, 0, n1=30, n2=25).

Habitat: On overwintered leaves of *Rubus idaeus* L., *Rubus* sp. L., and *R. spectabilis* Pursh. (Rosaceae).

Distribution: Canada (British Columbia) and Europe (Switzerland).

Materials examined: CANADA, BRITISH COLUMBIA: Manning Provincial Park, on overwintered leaves of *Rubus* sp., 13 May 2006, M.V. Sogonov (BPI 877559B, GenBank EU 254939); BRITISH COLUMBIA: Victoria Island, Route 14, on overwintered leaves of *Rubus spectabilis,* 10 May 2006, M.V. Sogonov (BPI 877638, GenBank EU 254938). SWITZERLAND: on overwintered leaves of *Rubus idaeus,* 21 May 2005, M.V. Sogonov (BPI 877637, GenBank EU 254937).

Notes: This species is one of nine that occur on hosts in the Rosaceae, and the only species of *Ophiognomonia* known to occur exclusively on *Rubus.* This species has the second longest perithecial neck length. Only *O. apiospora* has a longer perithecial neck in the genus *Ophiognomonia.*

Ophiognomonia sassafras (Ellis & Everh.) M. Monod, Beih. Sydowia 9: 157. 1983. Figure 42a–j.

Basionym: *Gnomonia sassafras* Ellis & Everh., Bull. Torrey bot. Club 10(7): 98. 1883.

≡ *Pleuroceras sassafras* (Ellis & Everh.) M.E. Barr, Mycol. Mem. 7: 122. 1978.

MycoBank: MB 108295

Perithecia immersed, occasionally causing host tissue to swell and rupture, on leaf blades and veins, hypophyllous or epiphyllous, solitary or loosely grouped, glossy black, globose to subglobose, (216–)217–278(–290) μm high×(279–)287–333(–345) μm diam (mean=249×279, S.D. 26, 90.8, n1=11, n2=12). Necks central to marginal, straight to slightly sinuous, (520–)543–950(–1,058) μm long (mean=

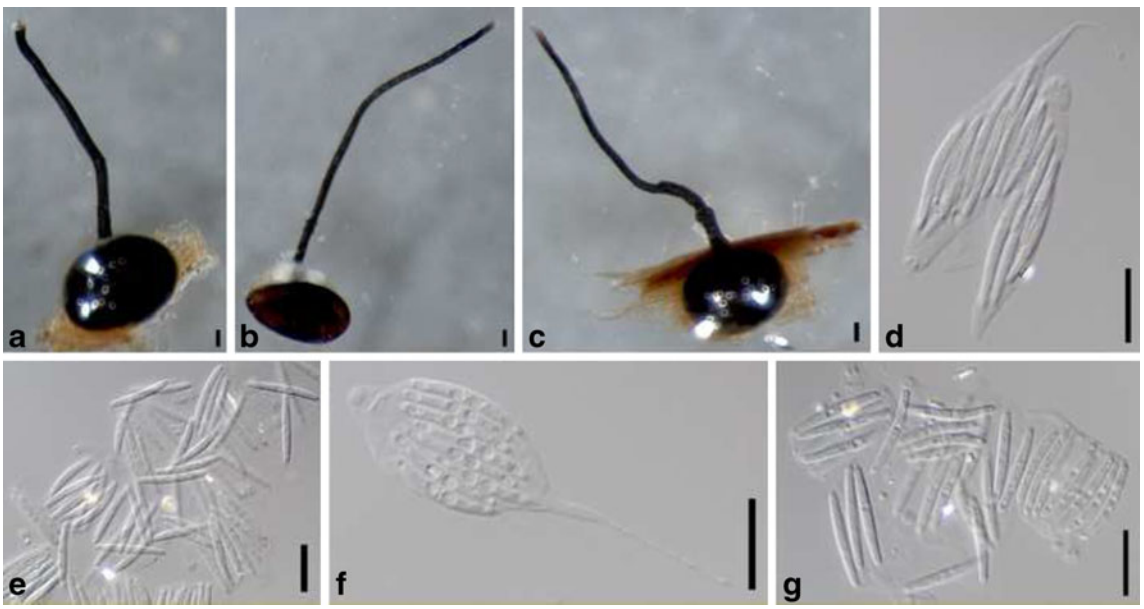

Fig. 41 *Ophiognomonia rubi-idaei*. **a**, **f**. BPI 877559B; **b**–**c**, **e**, **g**. BPI 877638; **d**. BPI 877637;. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

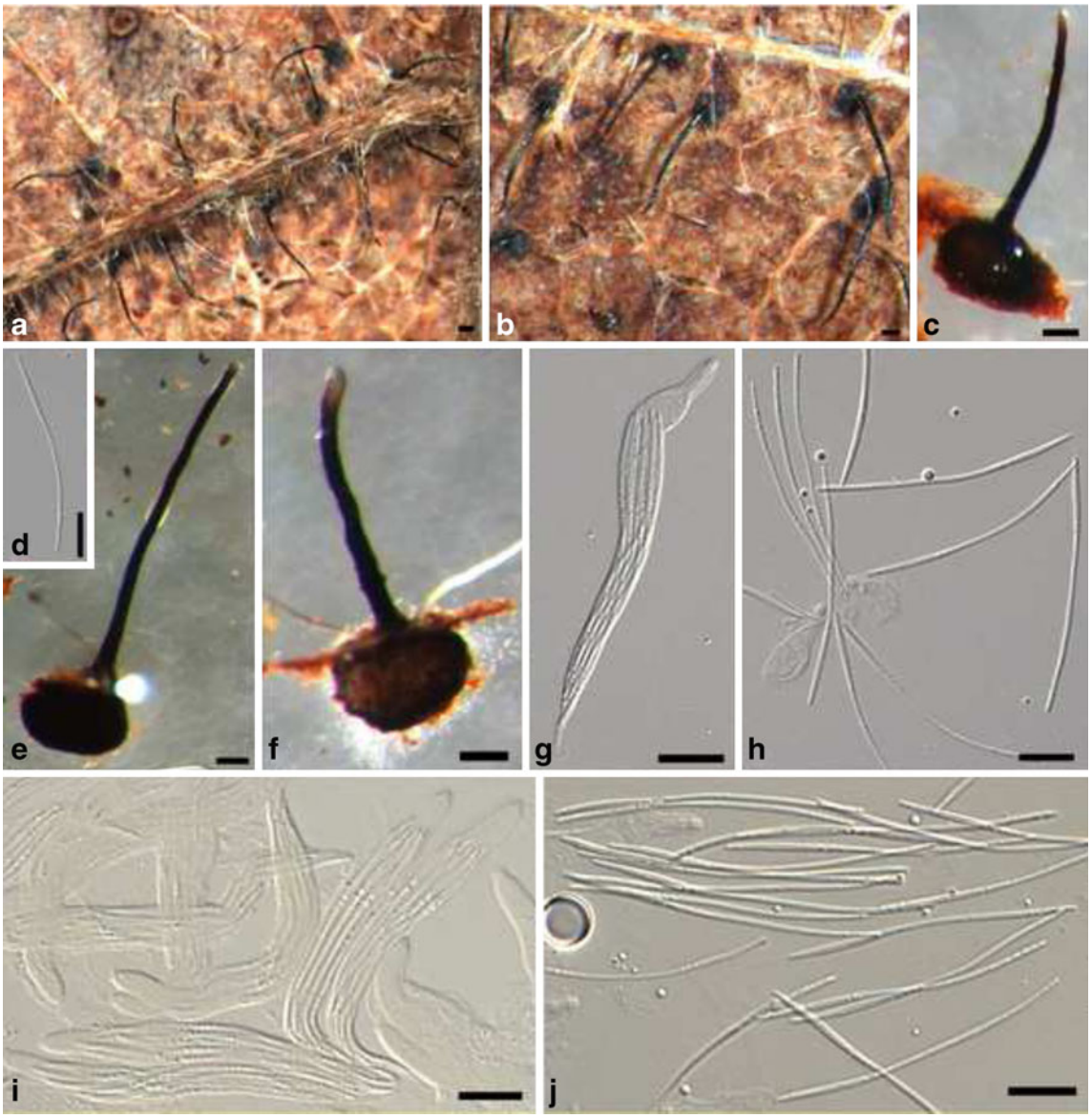

Fig. 42 *Ophiognomonia sassafras*. **a**–**c**, **i**. Holotype Ellis and Everhart 1684; **d**–**e**, **g**–**h**. BPI 882282; **f**, **j**. Epitype BPI 882285. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

776, S.D. 147, *n*=22). Asci narrowly fusiform, apex rounded, stipe rounded or tapering, apical ring conspicuous, (59–)62–68(–70)×(4–)5–7 μm (mean=66×6, S.D. 3.2, 1.2, n1=11, n2=11), ascospores arranged obliquely parallel. Ascospores clavately filiform to sinuous, rounded ends, one-septate, supramedian, not constricted at septum, basal cell narrower than distal cell, several small guttules, (42–)43–48(–52)×1–2 μm (mean=44×2, S.D. 8.6, 0.5, n1=30, n2=30).

Habitat: On overwintered leaves of *Sassafras albidum* (Nutt.) Nees and *S. officinale* Siebold (Lauraceae).

Distribution: United States (MD, OH, WV).

Materials examined: UNITED STATES, MARYLAND: Prince George's County, Beltsville Agricultural Research Center, on overwintered leaves of *Sassafras albidum,* 25 April 2010, D.M. Walker (BPI 882282, culture DMW 537); MARYLAND: Prince George's County, Beltsville Agricultural Research Center, on overwintered leaves of *Sassafras albidum,* 25 April 2010, D.M. Walker (BPI 882285, EPITYPE designated here, ex-epitype culture DMW 542=CBS 131366); OHIO: Fairfield County, fallen leaves of *Sassafras officinale,* May 1883, Kellerman (NY 00921946, HOLOTYPE of *Gnomonia sassafras*); WEST VIRGINIA: Pendleton County, Franklin, on overwintered leaves of *Sassafras albidum,* 2 April 2010, coll. C.M. Milensky, det. D.M. Walker (BPI 882284, culture DMW 541=CBS 131435).

Notes: *Ophiognomonia sassafras* is the only species of Gnomoniaceae known to occur on *Sassafras* in the Lauraceae and may represent a shift to a novel host family. The species *O. cordicarpa, O. longispora, O. melanostyla,* and *O. sassafras* share elongated filiform ascospores and form a clade of closely related species (Fig. 3).

Ophiognomonia setacea (Pers.: Fr.) Sogonov, Stud. Mycol. 62: 64. 2008. Figure 43a–f.

Basionym: *Sphaeria setacea* Pers.: Fr., Syn. Method. Fung. 62. 1801 : Syst. Mycol. 2: 517. 1823.

≡ *Gnomonia setacea* (Pers.: Fr.) Ces. & De Not., Comment. Soc. Crittog. Ital. 1: 232. 1863.

Habitat: On overwintered leaves of *Acer* sp., *Castanea dentata* L., *Castanea* sp., *Corylus* sp., *Fagus* sp., *Platanus* sp., *Quercus acutissima* Carruth., *Q. alba* L., *Q. bicolor* Willd., *Q. cerris* L., *Q. macrocarpa* Michx, *Q. montana* Willd., *Q. palustris* Münchh., *Q. phellos* L., *Q. pubescens* Willd., *Q. robur* L., and *Quercus* sp. (Betulaceae, Fagaceae, Platanaceae, Sapindaceae).

Distribution: Canada (Ontario), Europe (Austria, Bulgaria, Germany, Italy, Montenegro, Sweden, Switzerland), Japan (Ibaraki prefecture), and United States (LA, MD, MI, NJ, NY, OH, PA, TN, VA, WV).

Materials examined: JAPAN, IBARAKI: Tsukuba City, Botanical Garden, on overwintered leaves of *Quercus acutissima,* 5 April 2010, D.M. Walker (BPI 882212, culture DMW 333.2=CBS 131339); IBARAKI: Ushiku, Ushiku nature reserve, on overwintered leaves of *Quercus acutissima,* 9 April 2010, D.M. Walker (BPI 882223, culture DMW 358.4). UNITED STATES, MICHIGAN: Sanilac County, Lakeport campground, on overwintered leaves of *Quercus* sp., 27 May 2010, D.M. Walker (BPI 882275, culture DMW 510.1); NEW JERSEY: Middlesex County, New Brunswick, Kilmer reserve, on overwintered leaves of *Quercus palustris,* 24 April 2009, D.M. Walker (BPI 882204, culture DMW 289.1);

Notes: This is the only globally distributed species found in most temperate parts of the world. *Ophiognomonia setacea* and *O. michiganensis* are the only species of *Ophiognomonia* that occur on several different host plant families or orders. For a detailed description of this species, see Sogonov et al. (2008).

Ophiognomonia sogonovii D.M. Walker, sp. nov. Figure 44a–i.

MycoBank: MB 564105

Etymology: sogonovii was named after Mikhail Sogonov to honor his contribution to the taxonomy of the Gnomoniaceae.

Holotypus: JAPAN, IBARAKI: Tsukuba City, West side of Mt. Tsukuba, on overwintered leaves of *Quercus serrata,* 5

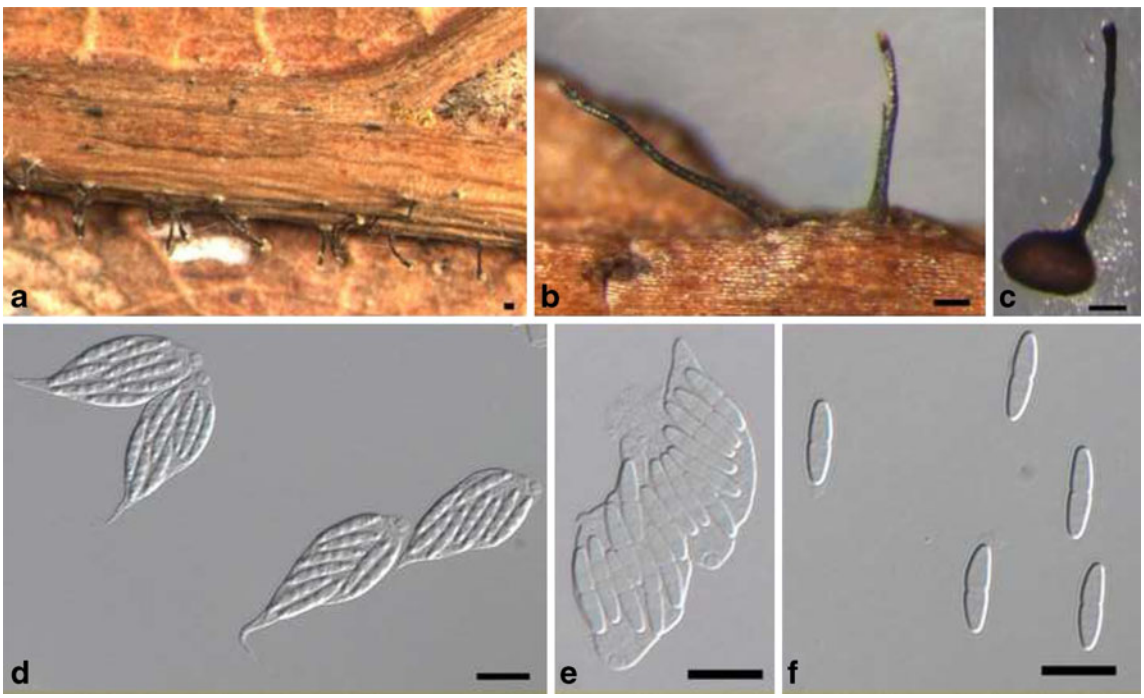

Fig. 43 *Ophiognomonia setacea*. **a**, **d**. BPI 882275; **b**. BPI 882204; **c**, **e**, **f**. BPI 882223. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

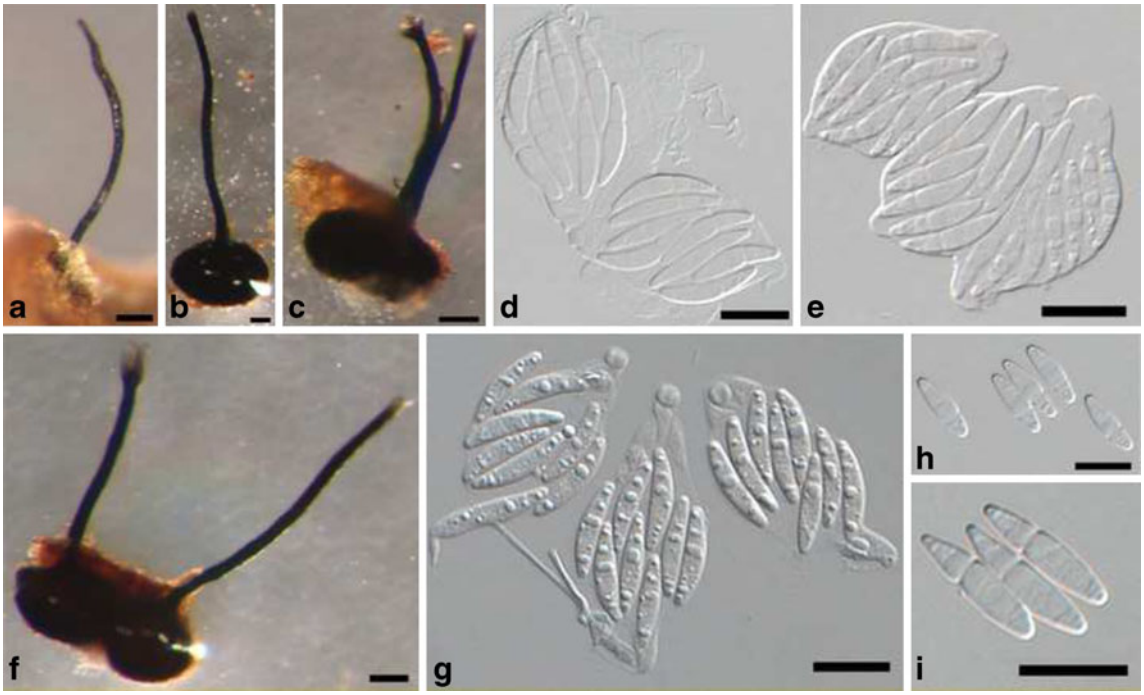

Fig. 44 *Ophiognomonia sogonovii*. **a**–**e**. BPI 882213; **f**–**i**. BPI 882221. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

April 2010, D.M. Walker (BPI 882214, ex-type culture DMW 337.1=CBS 131341).

Perithecia immersed, on leaf petioles, veins, and blades, solitary or aggregated up to two, glossy black, subglobose, (166–)188–294(–335) μm high×(204–)243–397(–498) μm diam (mean=224×322, S.D. 50.7, 81.2, n1=12, n2=11). Necks central to marginal, mostly straight or slightly curved, (513–)543–949(–1,172) μm long (mean=724, S.D. 184.5, *n*=13). Asci fusiform to ellipsoid, apex papillate or rounded, stipe tapering, apical ring large, conspicuous (22–)23–38(–39)× (11–)12–19(–20) μm (mean=32×15, S.D. 4.4, 2.4, n1=28, n2=28), ascospores arranged irregularly uniseriate or multiseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, distinctly submedian or supramedian, not constricted or slightly constricted at septum, each cell with 0–2 distinct or several small guttules, (12–)13–16(–17)×(2–)3–4 μm (mean=14×3, S.D. 1.4, 0.6, n1=30, n2=30).

Habitat: On overwintered leaves of *Quercus mongolica* Fisch. ex Turcz., *Q. mongolica* Fisch. ex Turcz., var. *grosseserrata* (Blume) Rehder & E.H. Wilson, and *Q. serrata* Murray (Fagaceae).

Distribution: Japan (Ibaraki and Nagano prefectures) and Russia (Primorsky Territory).

Materials examined: JAPAN, IBARAKI: Tsukuba City, West side of Mt. Tsukuba, on overwintered leaves of *Quercus mongolica,* 5 April 2010, D.M. Walker (BPI 882213, cultures DMW 336.1, DMW336.3=CBS 131340); NAGANO: Ueda-shi, Sugadaira, Arboretum at Sugadaira Montane Research Center, on overwintered leaves of *Quercus mongolica* var. *grosseserrata,* 13 April 2010, D.M. Walker (BPI 882221, culture DMW 353.1=CBS 131661). RUSSIA, PRIMORSKY TERRITORY: Russky Island, on dead leaves of *Quercus mongolica,* 25 May 2003, L.N. Vasilyeva (BPI 872323, culture CBS 121914).

Notes: This is one of four species of *Ophiognomonia* known to occur exclusively on *Quercus.* A group of closely related species including *O. asiatica, O. kobayashii, O. otanii,* and *O. sogonovii* are specific to *Quercus* spp. and *Castanea* spp. within the Fagaceae (Fig. 2).

Ophiognomonia trientensis (M. Monod) Sogonov, Stud. Mycol. 62: 64. 2008. Figure 45a–g.

Basionym: *Gnomonia trientensis* M. Monod, Beih. Sydowia 9: 90. 1983.

MycoBank: MB 512192

Perithecia immersed, occasionally causing host tissue to swell, on leaf blades and veins, hypophyllous and epiphyllous, solitary or aggregated up to two, glossy black to cream, subglobose, (134–)136–255(–264) μm high×(203–)213–364(–386) μm diam (mean=198×288, S.D. 62, 71.3, n1=

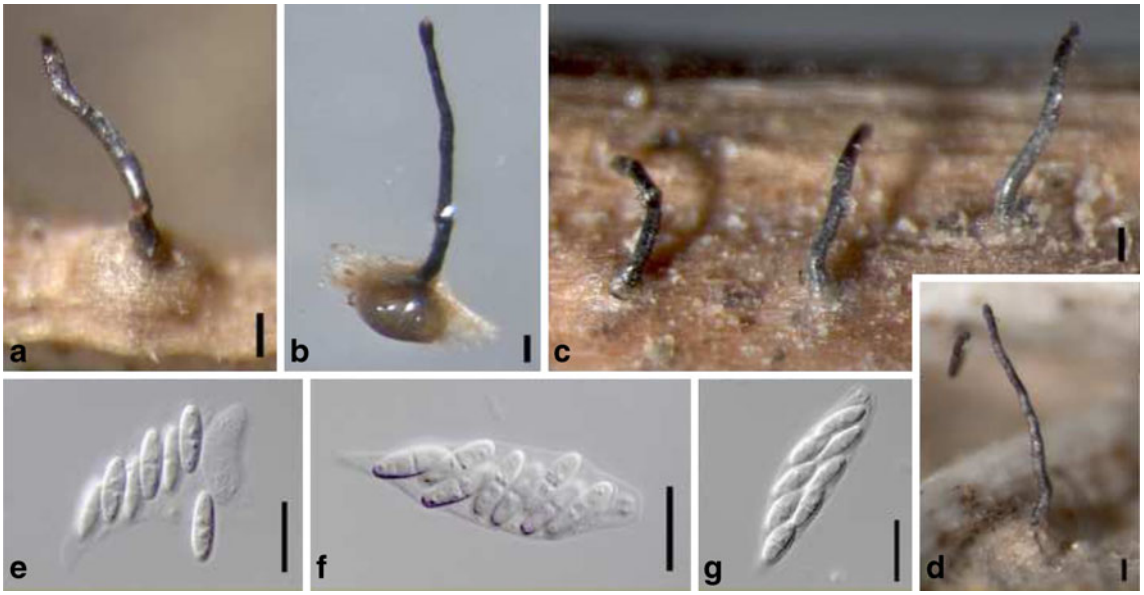

Fig. 45 *Ophiognomonia trientensis*. **a**, **c**. BPI 877673; **b**, **d**–**g**. BPI 877672. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

6, n2=8). Necks central, straight, curved, or contorted, (302–)326–1,019(–1,073) μm long (mean=597, S.D. 236, *n*=21). Asci ellipsoid to fusiform, apex rounded, stipe rounded to acute, (33–)35–41(–44)×(7–)8–10(–11) μm (mean=37×9, S.D. 3.9, 1.4, n1=8, n2=8), ascospores irregularly uniseriate, biseriate, overlapping. Ascospores oval to broadly fusiform with rounded ends, straight, one-septate, median to sub- or supramedian, not constricted at septum, each cell with two large and several small guttules, 9–10×3–4 μm (mean=10×3, S.D. 0.5, 0.3, n1=25, n2=20).

Habitat: On overwintered leaves of *Alnus tenuifolia* Nutt. and *A. viridis* (Chaix) DC. (Betulaceae).

Distribution: Canada (British Columbia), Europe (Switzerland), and United States (WA).

Materials examined: CANADA, BRITISH COLUMBIA: Hope, on overwintered leaves of *Alnus tenuifolia,* 13 May 2006, M.V. Sogonov (BPI 877672, GenBank EU 254986); BRITISH COLUMBIA: Manning Provincial Park, Engineers Trail, on overwintered leaves of *Alnus viridis,* 13 May 2006, M.V. Sogonov (BPI 877673, GenBank EU 254987). UNITED STATES, ALASKA: Kenai Peninsula County, In between Augustine Island, Shaw Island, and Kamishak Bay, on overwintered leaves of *Alnus* sp., 21 June 2011, D.M. Walker (BPI 882638, DMW 554=CBS 131604); WASHINGTON: King County, Mount Baker-Snoqualmie National Forest, Snoqualmie Ranger District, near exit 42 on highway US 90, on overwintered but still attached leaves of *Alnus viridis,* 16 May 2006, M.V. Sogonov (BPI 877674, GenBank EU 254985).

Notes: Only *O. gardiennetii* and *O. trientensis* are known to occur exclusively on *Alnus* from the U.S. Morphologically these species are very similar and can only be distinguished by DNA sequence data. In addition, they form a clade of closely related species with the butternut pathogen *O. clavigignenti-juglandacearum* (Fig. 4).

Ophiognomonia tucumanensis L.C. Mejía & D.M. Walker, sp. nov. Figure 46a–g.

MycoBank: MB 564106

Etymology: tucumanensis refers to the province of Tucuman where the holotype was collected.

Holotypus: ARGENTINA, TUCUMAN: on dead leaves of *Alnus acuminata,* 20 April 2011, A.Y. Rossman, det. D.M. Walker (BPI 882288, ex-type culture DMW 549=CBS 131364).

Perithecia immersed to erumpent, causing host tissue to swell, on leaf blades, veins, and petioles, hypophyllous and epiphyllous, solitary or loosely aggregated up to four, glossy black, globose to subglobose, (198–)203–277(–285) μm high×(191–)202–296(–320) μm diam (mean=238×257, S.D. 28.2, 40.3, n1=10, n2=10). Necks central to marginal, straight, curved, or slightly sinuous, neck base occasionally disc shaped, (298–)436–1,056(–1,059) μm long (mean=756, S.D. 213, *n*=24). Asci ellipsoid to fusiform with rounded apex, stipe acute

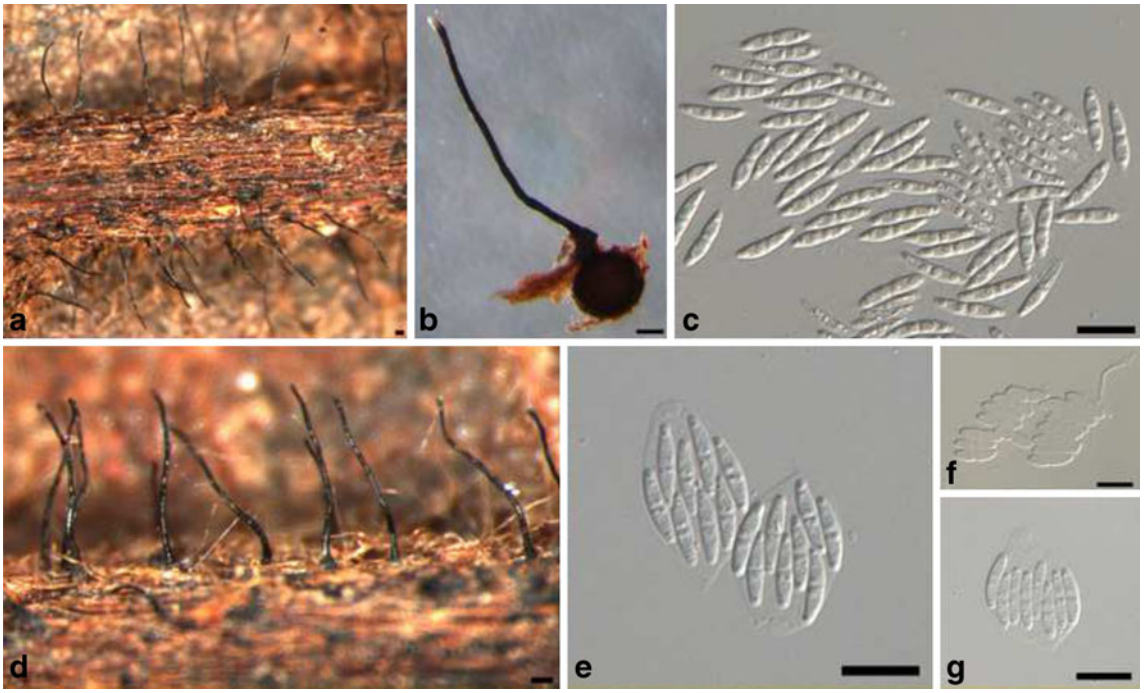

Fig. 46 *Ophiognomonia tucumanensis.* **a**–**d**, **f**. Holotype BPI 882288; **e**, **g**. BPI 879565. Scale bars of perithecia=100 μm. Scale bars of asci and ascospores=10 μm

or short tapering, apical ring sometimes conspicuous, (21–)22–29(–32)×(11–)12–16(–17) μm (mean=25×14, S.D. 2.6, 1.4, n1=26, n2=25), ascospores arranged irregularly uniseriate to multiseriate. Ascospores fusiform with rounded ends, straight to slightly curved, one-septate, median to indistinctly sub- or supramedian, slightly to not constricted at septum, each cell with 0–2 large and several small guttules, (9–)10–12(–13)×2–3(–4) μm (mean=12×3, S.D. 1.2, 0.4, n1=30, n2=30).

Habitat: On dead leaves of *Alnus acuminata* Kunth (Betulaceae).

Distribution: Argentina (Tucuman).

Materials examined: ARGENTINA, TUCUMAN: Villa Nougues, dead leaves of *Alnus acuminata,* 16 November 2008, L.C. Mejía, det. D.M. Walker (BPI 879565, culture LCM 622.01=CBS 131368).

Notes: *Ophiognomonia tucumanensis* is the only species of Gnomoniaceae known from South America on *Alnus acuminata.* This plant host occurs in montane cloud forests from Mexico to the Andes. *Ophiognomonia tucumanensis* represents the southernmost distribution of the Gnomoniaceae. Only *O. bugabensis* and *O. tucumanensis* are known to occur on *Alnus acuminata.* These species can be distinguished by geographic location. In addition, *O. bugabensis* has larger ascospores and shorter perithecial necks than *O. tucumanensis.*

Ophiognomonia vasiljevae Sogonov, Stud. Mycol. 62: 53. 2008.

Habitat: On overwintered leaves of *Juglans nigra* L. and *Juglans* sp. L. (Juglandaceae).

Distribution: United States (MD, TN, VA).

Materials examined: UNITED STATES, MARYLAND: Frederick and Carroll Counties, Patapsco State Park, on overwintered leaves of *Juglans* sp., 11 April 2011, D.M. Walker (BPI 882289, culture DMW 550=CBS 131436); TENNESSEE: Blount County, Great Smoky Mountains National Park, along loop near Methodist Church, on leaves of *Juglans nigra*, 24 May 2006, M.V. Sogonov (HOLOTYPE, BPI 877671, ex-type culture CBS 121253); VIRGINIA: Fairfax County, Burke, Zion Rd. and Guinea Rd., on leaves of *Juglans nigra*, 1 June 2009, M.V. Sogonov (BPI 882206, culture DMW 303.3=CBS 128353).

Notes: This is one of three species that occur on *Juglans.* Several other species are known to occur on *Carya* and *Juglans* in the Juglandaceae including the pathogens *O. leptostyla* and *O. clavigignenti-juglandacearum.* For a detailed description of this species, see Sogonov et al. (2008).

Synoptic key to species in *Ophiognomonia*

Perithecia

1. Average Height

100–200 μm 1, 12, 14, 16, 18, 19, 26, 31, 34, 37, 43
200–300 μm 2, 4, 6, 8, 9, 10, 13, 15, 17, 20, 21, 22, 23, 24, 27, 29, 30, 32, 35, 36, 38, 40, 42, 44, 41
300–400 μm 3, 5, 11, 25, 28, 45, 33
400–500 μm 39

2. Average Diameter

100–200 μm 14, 18, 26, 31
200–300 μm 1, 2, 9, 12, 13, 15, 16, 19, 20, 22, 24, 34, 37, 40, 43, 44
300–400 μm 4, 6, 10, 11, 17, 21, 23, 27, 29, 30, 32, 35, 36, 38, 42, 41
400–500 μm 5, 8, 25, 28
500–600 μm 39, 33
600–700 μm 45
700–800 μm 3

Perithecial Neck

1. Average Length

100–200 μm 34
200–300 μm 1
300–400 μm 11, 12, 13, 19, 25, 31, 37
400–500 μm 6, 9, 16, 18, 20, 26
500–600 μm 13, 17, 24, 36, 43
600–700 μm 15, 28, 35, 38, 45, 41
700–800 μm 4, 21, 22, 32, 40, 42, 44
800–900 μm 29
900–1,000 μm 5, 8, 27, 33
1,000–1,100 μm 2, 23
1,100–1,200 μm 30
1,400–1,500 μm 10, 39
2,200–2,300 μm 3

Ascospores

1. Shape

filiform 8, 21, 23, 40, 33
fusiform 1, 2, 3, 4, 5, 9, 10, 11, 12, 13, 15, 16, 17, 18, 20, 22, 24, 26, 27, 28, 30, 31, 32, 35, 36, 37, 38, 39, 42, 44, 45, 41
broadly fusiform 6, 25, 43
broadly ellipsoid 34
oval 14, 19
lenticular 29

2. Septation

aseptate 29
one-septate 1, 2, 3, 4, 5, 6, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 30, 31, 32, 34, 35, 36, 37, 38, 39, 40, 42, 43, 44, 45, 33, 41

3. Location of Septation

submedian 1, 3, 10, 11, 24, 32, 42
median . . . 2, 4, 5, 14, 15, 16, 17, 18, 19, 20, 22, 25, 26, 27, 28, 30, 31, 34, 35, 36, 37, 38, 39, 43, 44, 45, 33, 41
supramedian 6, 8, 9, 12, 13, 21, 23, 40, 42

4. Appendages

present 5, 10, 13, 15, 16, 21, 23, 24, 30, 34, 35, 41
absent. 1, 2, 3, 4, 6, 8, 9, 11, 12, 14, 17, 18, 19, 20, 22, 25, 26, 27, 28, 29, 31, 32, 36, 37, 38, 39, 40, 42, 43, 44, 45, 33

5. Average Length

5–10 μm 19, 34, 43
10–15 μm. 2, 4, 9, 11, 13, 14, 15, 17, 18, 20, 22, 24, 26, 27, 29, 31, 37, 44, 41
15–20 μm. 5, 6, 10, 12, 16, 30, 32, 35, 36, 38, 39, 42, 45
20–25 μm. 1, 28
25–30 μm. 3
35–40 μm. 21, 23, 25, 40
45–50 μm. 33
60–65 μm. 8

6. Average Width

0–1 μm 8, 21, 23, 33
1–2 μm 10, 30, 39, 40, 41
2–3 μm 2, 4, 5, 9, 11, 12, 13, 15, 16, 17, 18, 19, 20, 22, 24, 26, 27, 31, 32, 34, 35, 38, 44, 45
3–4 μm 3, 14, 28, 36, 37, 42, 43
4–5 μm 6
5–6 μm 1, 29
6–7 μm 25

Host Plant

Alnus acuminata 6, 44
Alnus cordata 1
Alnus firma 27
Alnus nepalensis 3
Alnus serrulata 9
Alnus spp. 2, 14, 15, 24, 28, 35, 43
Betula lutea 13
Betula maximowicziana 22
Betula nana 29
Betula pubescens. 35
Betula spp. 15, 24
Carpinus americana 24
Carpinus betulus 16
Carpinus spp. 26
Carya spp. 25
Castanea crenata 18
Castanea spp. 41
Corylus avellana 16
Fragaria vesca 10, 38
Geum pyrenaicum. 10

1. *Ophiognomonia alni-cordatae*
2. *Ophiognomonia alni-viridis*
3. *Ophiognomonia apiospora*
4. *Ophiognomonia asiatica*
5. *Ophiognomonia balsamiferae*
6. *Ophiognomonia bugabensis*
7. *Ophiognomonia clavigignenti-juglandacearum*
8. *Ophiognomonia cordicarpa*
9. *Ophiognomonia gardiennetii*
10. *Ophiognomonia gei*
11. *Ophiognomonia gei-montani*
12. *Ophiognomonia gunmensis*
13. *Ophiognomonia hiawathae*
14. *Ophiognomonia ibarakiensis*
15. *Ophiognomonia intermedia*
16. *Ophiognomonia ischnostyla*
17. *Ophiognomonia japonica*
18. *Ophiognomonia kobayashii*
19. *Ophiognomonia lenticulispora*
20. *Ophiognomonia leptostyla*
21. *Ophiognomonia longispora*
22. *Ophiognomonia maximowiczianae*
23. *Ophiognomonia melanostyla*
24. *Ophiognomonia michiganensis*
25. *Ophiognomonia micromegala*
26. *Ophiognomonia monticola*
27. *Ophiognomonia multirostrata*
28. *Ophiognomonia naganoensis*
29. *Ophiognomonia nana*
30. *Ophiognomonia nipponicae*
31. *Ophiognomonia ostryae-virginianae*
32. *Ophiognomonia otanii*
33. *Ophiognomonia padicola*
34. *Ophiognomonia pseudoclavulata*
35. *Ophiognomonia pseudoischnostyla*
36. *Ophiognomonia pterocaryae*
37. *Ophiognomonia quercus-gambellii*
38. *Ophiognomonia rosae*
39. *Ophiognomonia rubi-idaei*
40. *Ophiognomonia sassafras*
41. *Ophiognomonia setacea*
42. *Ophiognomonia sogonovii*
43. *Ophiognomonia trientensis*
44. *Ophiognomonia tucumanensis*
45. *Ophiognomonia vasiljevae*

Excluded or doubtful names in *Ophiognomonia*:

Ophiognomonia capillaris (Penz. & Sacc.) M. Monod, Beih. Sydowia 9: 160. 1983.

Basionym: *Linospora capillaris* Penz. & Sacc., Malpighia 11: 409. 1904.
= *Linospora liquidambaris* Teng, Sinensia 4: 384. 1934.

Holotypus: JAVA: Tjibodas, on dead leaves of undetermined host (PAD-not examined). Also, reported from China on *Liquidambar formosana* by Teng (1934).

Notes: Monod (1983) examined the type and second specimen of this taxon. Based on his description of ascomata with very long perithecial necks, 1,100–1,600 μm long, and elongated ascospores, 49–58×1–1.2 μm, it is possible that this species belongs in *Ophiognomonia*, however, it was not encountered during this study. The most well-known species of the Gnomoniaceae on *Liquidambar* is *Ambarignomonia petiolorum,* which has ascomata each with a thin, elongated perithecial neck surrounded by a white collar at the base and 9–15×1.5–2 μm, one-septate ascospores, quite unlike the description of *O. capillaris* (Sogonov et al. 2008).

Ophiognomonia caulicola Hohn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 117: 1213. 1908.

Holotypus: AUSTRIA: bei Ybbsitz, on dead branch of *Salvia glutinosa*, April 1909, Strasser (FH-not examined).

Notes: Monod (1983) examined the depauperate type specimen and provided a partial description of this species. This host is unusual for a member of the Gnomoniaceae and it seems doubtful that this species belongs in that family. It is known only from the type specimen.

Ophiognomonia cryptica D. Wilson & M.E. Barr in Wilson, Barr & Faeth, Mycologia 89: 539. 1997.

Holotypus: UNITED STATES, ARIZONA: Pinal Co., 100 km E of Phoenix, alt. 1,292 ft, isolated from leaves of *Quercus emoryi,* December 1994, D. Wilson (BPI 749237).

Notes: This species was isolated as an endophyte of *Quercus emoryi* and produced ascomata in culture. The holotype specimen that consists of five dried cultures labeled with differing numbers was examined superficially. Based on the description, the ascomata have long beaks 400–1,400 μm and filiform ascospores 38–48 × 2–2.5 μm. These characteristics suggest that this species belongs in *Ophiognomonia*; however, no living material was encountered during this study. Attempts to obtain DNA and sequence data from the dried culture of the holotype specimen produced only that of contaminants.

Ophiognomonia elasticae (Koord.) M. Monod, Beih. Sydowia 9: 157. 1983.

Basionym: *Linospora elasticae* Koord., Botan. Untersuch. 193. 1907.

Holotypus: JAVA: on leaves of *Ficus elastica* (not examined).

Materials examined: PHILIPPINES: Province Laguna, near Los Banos, Mount Maquiling, on dead leaves of *Ficus* sp., June 1914, Baker, (Rehm Fungi Malayan 151, BPI 626855).

Notes: This species was described from Java, later reported from the Philippines (Teodoro 1937), and recently noted as the dominant fungus isolated from fallen leaves of *Ficus pleurocarpa* in Australia (Paulus et al. 2007). Monod (1983) examined a non-type specimen and retained it in *Ophiognomonia*; however, we examined that same specimen and concluded that this species should be placed in the genus *Ophiobolous* (Walker 1980) because of the lack of an apical ring in the ascus and the multiseptate, filiform ascospores. Cultures of this species from Australia were sequenced but proved to be basidiomycetes.

Ophiognomonia helvetica Rehm, Annls mycol. 5(6): 543. 1907.
≡ *Pleuroceras helvetica* (Rehm) Barr, Mycologia Memoir 7:121. 1978.

Holotypus: SWITZERLAND: on dead leaves of *Salix herbacea* (S-not examined).

Notes: Based on a specimen from northern Quebec, Barr (1978) placed this name in *Pleuroceras* stating that this is a "subarctic-subalpine species". Monod (1983) examined the type specimen from a high elevation in Switzerland and agreed with this placement, thus we accept this species as *P. helvetica*.

Ophiognomonia langii M. Monod, Sydowia Beih. 9: 156. 1983.

Holotypus: NORWAY: Tromso, on dead leaves of *Salix reticulate*, 19 July 1977, M. Monod (Monod 373 LAU-not examined).

Notes: Based on the description in Monod (1983), it seems likely that this arctic-alpine species belongs in *Pleuroceras*, related to *P. helvetica* mentioned above. This species has also been reported from Sweden (Eriksson 1992).

Ophiognomonia lapponica Vestergr., Bot. Notiser: 125. 1902.

Holotypus: SWEDEN: Lapponia, Lulensis, Lulleketje, Randijaure, on leaves of *Betula odorata*, 19 June 1900, C. Skottsberg and T. Vestergren (Vestergren Micromycetes Rariores Selecti 408, BPI 626912).

Notes: Based on an examination of the type specimen, this species could be accepted in the Gnomoniaceae in either *Ophiognomonia* or *Pleuroceras*. The basally immersed ascomata are relatively thick-walled, collapsing from the bottom when dry, each with a beak 200–300 × 60–120 μm. The ascospores are very thin, 65–75 × 1.5–2 μm, one-septate. No living material of this species was encountered.

Ophiognomonia procumbens (Fuckel) Berl., Icon. Fung. 2: 146. 1900.

Basionym: *Linospora procumbens* Fuckel, Jb. nassau. Ver. Naturk. 23–24: 124. 1870.

Notes: Monod (1983) examined type material of *L. procumbens* and suggested that this name is a synonym of *Pleuroceras pleurostylum* (Auersw.) Barr. This species is known to occur only on *Salix* in Europe, thus the reports of *O. procumbens* in California on dead leaves of *Quercus agrifolia* (French, 1980) are erroneous.

Ophiognomonia pseudoplatani (Tubeuf) D.K. Barrett & R.B. Pearce, Trans. Br. mycol. Soc. 76(2): 317. 1981.

Basionym: *Gnomonia pseudoplatani* Tubeuf, Z. PflKrankh. 40: 364. 1930.
≡ *Pleuroceras pseudoplatani* (Tubeuf) M. Monod, Beih. Sydowia 9: 171. 1983.
= *Asteroma pseudoplatani* Butin & Wulf, Sydowia 40: 39. 1987.

Holotypus: GERMANY: on fallen leaves of *Acer pseudoplatanus* (not examined).

Notes: Based on the description in Barrett and Pearce (1981), *Pleuroceras pseudoplatani* occurs in Europe and has ascospores 45–65 × 0.5 × 1.5 μm that resemble in shape but are longer than those of *P. tenellum* in North America having ascospores 20–36 × 1–2 μm. Ascospores of both species are elongate, slightly narrowing toward one septum with long appendages at each end (Barr 1978), characteristic of many species of *Pleuroceras* (Monod 1983). This species should be referred to as *Pleuroceras pseudoplatani* and causes a disease called giant leaf blotch of sycamore as described and illustrated by Barrett and Pearce (1981) and Butin and Wulf (1987).

Ophiognomonia sacchari Speg., Revta Fac. Agron. Vet. Univ. nac. La Plata 2(19): 231. 1896.

Holotypus: Argentina, Tucuman, on weakened leaves and sheath of *Saccharum officinalis* (LPS-not examined).

Notes: Nothing except the type description and specimen is known about this name but it seems unlikely as a member of the Gnomoniaceae.

Ophiognomonia umbelliferarum (M.E. Barr) Lar. N. Vassiljeva, Pyrenomycetes of the Russian Far East, 1. Gnomoniaceae (Vladivostok): 39 (1993).

Basionym: *Linocarpon umbelliferarum* M.E. Barr, Can. J. Bot. 39: 320. 1961.
≡ *Plagiosphaera umbelliferarum* (M.E. Barr) M.E. Barr, Mycol. Mem. 7: 123. 1978.

Holotypus: CANDA: Quebec, on dead stems of *Heracleum lanatum,* M.E. Barr (Barr 2198A-not examined).

Notes: This species is known only from the type specimen. The description and illustration of this species by Barr (1961) show a refractive, globular cluster in the ascal apex characteristic of genera in the Sordariales such as *Lasiosphaeria* and *Neolinocarpon*, thus it is unrelated to *Ophiognomonia*. Walker (1980) considered this species to be similar to *Plagiosphaera immersa* (≡ *Ophiobolus immersa*), but could not distinguish them. A GenBank BLAST search of the ITS region (ITS1, 5.8 S rDNA and ITS2) of *P. immersa*, type of *Plagiosphaera*, suggests that this genus belongs outside of the Gnomoniaceae, rather it is distantly related to *Gaeumannomyces* in the Magnaporthales (on *Urtica dioica* from Veronnes, France, culture BPI 883014, culture DMW 571).

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References

Aguileta G, Marthey S, Chiapello H, Lebrun M-H, Rodolphe F, Fournier E, Gendrault-Jacquemard A, Giraud T (2008) Assessing the performance of single-copy genes for recovering robust phylogenies. Syst Biol 57(4):613–627. doi:10.1080/10635150802306527

Anderson RL, LaMadeleine LA (1978) The distribution of butternut decline in the eastern United States. Forest Survey Report USDA Forest Service, p. 5

Avise JC, Ball RM Jr (1990) Principles of genealogical concordance in species concepts and biological taxonomy. In: Oxford surveys in evolutionary biology, vol 7. Oxford Univ. Press, Oxford

Barr ME (1978) The diaporthales in North America with emphasis on *Gnomonia* and its segregates. Mycol Mem 7:1–232

Barrett DK, Pearce RB (1981) Giant leaf blotch disease of sycamore (*Acer pseudoplatanus*) in Britain. Trans Brit Mycol Soc 76:317–345

Behdad E (1991) Plant protection encyclopedia of Iran: pests, diseases, and weeds. Yad-boud Publisher, Isfahan

Belisario A, Scotton M, Santori A, Onofri S (2008) Variability in the Italian population of *Gnomonia leptostyla*, homothallism and resistance of *Juglans* species to anthracnose. For Pathol 38 (2):129–145. doi:10.1111/j.1439-0329.2007.00540.x

Berry FH (1981) Walnut anthracnose forest insect & disease leaflet 85. US Department of Agriculture, Forest Service, Northern Area State & Private Forestry, Broomall

Broders KD, Boland GJ (2011) Reclassification of the butternut canker fungus, *Sirococcus clavigignenti-juglandacearum*, into the genus *Ophiognomonia*. Fungal Biol 115(1):70–79

Broughton RE, Harrison RG (2003) Nuclear gene genealogies reveal historical, demographic and selective factors associated with speciation in field crickets. Genetics 163(4):1389–1401

Butin H, Wulf A (1987) *Asteroma pseudoplatani* sp. nov., anamorph of *Pleuroceras pseudoplatani* (v. Tubeuf) Monod. Sydowia 40:38–41

Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol Biol Evol 17(4):540–552

Cummings MP, Neel MC, Shaw KL (2008) A genealogical approach to quantifying lineage divergenece. Evolution 62(9):2411–2422. doi:10.1111/j.1558-5646.2008.00442.x

Damm U, Crous PW, Fourie PH (2007) Botryosphaeriaceae as potential pathogens of *Prunus* species in South Africa, with descriptions of *Diplodia africana* and *Lasiodiplodia plurivora* sp. nov. Mycologia 99(5):664–680. doi:10.3852/mycologia.99.5.664

Dettman JR, Jacobson DJ, Taylor JW (2003) A multilocus genealogical approach to phylogenetic species recognition in the model eukaryote *Neurospora*. Evolution 57(12):2703–2720. doi:10.1111/j.0014-3820.2003.tb01514.x

Eriksson OE (1992) The non-lichenized pyrenomycetes of Sweden. Btjtryck, Lund, p 208

Green S (2004) Fungi associated with shoots of silver birch (*Betula pendula*) in Scotland. Mycol Res 108:1327–1336

Green S, Castlebury LA (2007) Connection of *Gnomonia intermedia* to *Discula betulina* and its relationship to other taxa in Gnomoniaceae. Mycol Res 111:62–69

Hillis DM, Dixon MT (1991) Ribosomal DNA: molecular evolution and phylogenetic inference. Q Rev Biol 66(4):411–453

Hudson RR, Coyne JA (2002) Mathematical consequences of the genealogical species concept. Evolution 56(8):1557–1565. doi:10.1111/j.0014-3820.2002.tb01467.x

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755

Johnson LA, Soltis DE (1998) Assessing congruence: empirical examples from molecular data. In: Soltis DE, Soltis PS, Doyle JJ (eds) Molecular systematics of plants 2. Kluwer, U.S.A., pp 287–348

Juhasova G, Ivanova H, Spisak J (2006) Biology of fungus *Gnomonia leptostyla* in agro-ecological environments of Slovakia. Mikol Fitopatol 40:538–547

Kellogg EA, Appels R, Mason-Gamer RJ (1996) When genes tell different stories: the diploid genera of Triticeae (Graminae). Syst Bot 21:321–347

Kobayashi T (1970) Taxonomic studies of Japanese Diaporthaceae with special reference to their life-histories. Bulletin of the Government Forest Experiment Station 226:1–242

Letcher PM, Powell MJ, Viusent MC (2008) Rediscovery of an unusual chytridiaceous fungus new to the order Rhizophydiales. Mycologia 100(2):325–334. doi:10.3852/mycologia.100.2.325

Mason-Gamer RJ, Kellogg EA (1996) Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae. Syst Biol 45:524–545

Mejía LC, Castlebury LA, Rossman AY, Sogonov MV, White JF (2008) Phylogenetic placement and taxonomic review of the genus *Cryptosporella* and its synonyms *Ophiovalsa* and *Winterella* (Gnomoniaceae, Diaporthales). Mycol Res 112 (1):23–35

Mejía L, Rossman A, Castlebury L, Yang Z, White J (2011a) *Occultocarpon*, a new monotypic genus of Gnomoniaceae on *Alnus nepalensis* from China. Fungal Divers 52(1):99–105. doi:10.1007/s13225-011-0108-y

Mejia LC, Rossman AY, Castlebury LA, White JF Jr (2011b) New species, phylogeny, host-associations, and geographic distribution of the genus *Cryptosporella* (Gnomoniaceae, Diaporthales). Mycologia 103:379–399. doi:10.3852/10-134

Mejía LC, Castlebury LA, Rossman AY, Sogonov MV, White JF (2011c) A systematic account of the genus *Plagiostoma* (Gnomoniaceae, Diaporthales) based on morphology, host-associations, and a four-gene phylogeny. Stud Mycol 68(1):211–235. doi:10.3114/sim.2011.68.10

Monod M (1983) Monographie taxonomique des Gnomoniaceae (Ascomycétes de l'ordre des Diaporthales I). Beihefte zur Sydowia 9:1–315

Neely D, Black WM (1976) Anthracnose of black walnuts in the Midwest. Plant Dis Rep 60:519–521

Nixon KC, Carpenter JM (1993) On outgroups. Cladistics 9:413–426

O'Donnell K, Ward TJ, Geiser DM, Corby Kistler H, Aoki T (2004) Genealogical concordance between the mating type locus and seven other nuclear genes supports formal recognition of nine phylogenetically distinct species within the *Fusarium graminearum* clade. Fungal Genet Biol 41(6):600–623

Otani Y (1995) Mycological Flora of Japan. Vol III Ascomycotina No 3 Sordariales, Diaporthales Tokyo, Yokendo LTD, p. 310

Paulus B, Gadek P, Hyde K (2007) Successional patterns of microfungi in fallen leaves of *Ficus pleurocarpa* (Moraceae) in an Australian tropical rain forest. Biotropica 38:42–51

Pennycook SR (2007) *Discula betulae* comb. nov., correct name for the anamorph of *Gnomonia intermedia*. Mycotaxon 101:361–364

Pringle A, Baker DM, Platt JL, Wares JP, Latgé JP, Taylor JW (2005) Cryptic Speciation in the Cosmopolitan and Clonal Human Pathogenic Fungus *Aspergillus Fumigatus*. Evolution 59 (9):1886–1899. doi:10.1111/j.0014-3820.2005.tb01059.x

Raja HA, Miller AN, Shearer CA (2008) Freshwater ascomycetes: *Aquapoterium pinicola*, a new genus and species of Helotiales (Leotiomycetes) from Florida. Mycologia 100(1):141–148. doi:10.3852/mycologia.100.1.141

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19(12):1572–1574. doi:10.1093/bioinformatics/btg180

Rosenberg NA, Harrison R (2003) The shapes of neutral gene genealogies in two species: probabilities of monophyly, paraphyly, and polyphyly in a coalescent model. Evolution 57(7):1465–1477. doi:10.1554/03-012

Salahi S, Javan Nikkhah M, Jamshidi S (2009) Study on population structure of *Gnomonia leptostyla*, causal agent of walnut anthracnose in East Azarbaijan province, Iran. New Agric Sci J 3:53–68

Sarver BAJ, Ward TJ, Gale LR, Broz K, Corby Kistler H, Aoki T, Nicholson P, Carter J, O'Donnell K (2011) Novel *Fusarium* head blight pathogens from Nepal and Louisiana revealed by multilocus genealogical concordance. Fungal Genet Biol 48(12):1096–1107

Schmitt I, Crespo A, Divakar PK, Fankhauser JD, Herman-Sackett E, Kalb K, Nelsen MP, Nelson NA, Rivas-Plata E, Shimp AD, Widhelm T, Lumbsch HT (2009) New primers for promising single-copy genes in fungal phylogenetics and systematics. Persoonia 23:35–40

Sogonov MV, Castlebury LA, Rossman AY, White JF (2007) The type of species of *Apiognomonia*, *Apiognomonia veneta*, with its *Discula anamorph* is distinct from *Apiognomonia errabunda*. Mycol Res 111:693–709

Sogonov MV, Castlebury LA, Rossman AY, Mejía LC, White JF (2008) Leaf-inhabiting genera of the Gnomoniaceae, Diaporthales. Stud Mycol 62:1–77

Spatafora JW, Sung G-H, Johnson D, Hesse C, O'Rourke B, Serdani M, Spotts R, Lutzoni F, Hofstetter V, Miadlikowska J, Reeb V, Gueidan C, Fraker E, Lumbsch T, Lucking R, Schmitt I, Hosaka K, Aptroot A, Roux C, Miller AN, Geiser DM, Hafellner J, Hestmark G, Arnold AE, Budel B, Rauhut A, Hewitt D, Untereiner WA, Cole MS, Scheidegger C, Schultz M, Sipman H, Schoch CL (2006) A five-gene phylogeny of Pezizomycotina. Mycologia 98(6):1018–1028. doi:10.3852/mycologia.98.6.1018

Sullivan J (1996) Combining data with different distributions of among-site rate variation. Syst Biol 45(3):375–380. doi:10.1093/sysbio/45.3.375

Swofford DL (2002) PAUP 4.0b10: phylogenetic analysis using parsimony. Sinauer Associates, USA

Tajima F (1983) Evolutionary relationship of DNA sequences in finite populations. Genetics 105:437–460

Talavera G, Castresana J (2007) Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Syst Biol 56(4):564–577. doi:10.1080/10635150701472164

Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC (2000) Phylogenetic species recognition and species concepts in fungi. Fungal Genet Biol 31(1):21–32

Teodoro NG (1937) An enumeration of Philippine fungi. Techn Bull Dept Agric Comm Manila 4:1–585

Townsend JP (2007) Profiling phylogenetic informativeness. Syst Biol 56(2):222–231. doi:10.1080/10635150701311362

Townsend JP, Leuenberger C (2011) Taxon sampling and the optimal rates of evolution for phylogenetic inference. Syst Biol. doi:10.1093/sysbio/syq097

von Höhnel F (1919) Mycologische fragmenta. Ann Mycol 17:114–133

Walker J (1980) *Gaeumannomyces*, *Linocarpon*, *Ophiobolus* and several other genera of scolecospored ascomycetes and *Phialophora* conidial states, with a note on hyphopodia. Mycotaxon 11:1–129

Walker DM, Castlebury LA, Rossman AY, Sogonov MV, White JF Jr (2010) Systematics of the genus *Gnomoniopsis* (Gnomoniaceae, Diaporthales) based on a three gene phylogeny, host associations, and morphology. Mycologia 102(6):1479–1496. doi:10.3852/10-002

Walker DM, Castlebury LA, Rossman AY, White JF Jr (2012) New molecular markers for fungal phylogenetics: two genes for species-level systematics in the Sordariomycetes (Ascomycota). Mol Phylogenet Evol 64:500–512

Wild AL, Maddison DR (2008) Evaluating nuclear protein-coding genes for phylogenetic utility in beetles. Mol Phylogenet and Evol 48(3):877–891

Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas at Austin, USA