Cadophora Species from Marine Glaciers in the Qinghai-Tibet Plateau

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Research

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Abstract

Large numbers of marine glaciers in the Qinghai-Tibet Plateau are especially sensitive to changes of climate and surface conditions and they have suffered fast accumulation and melting and retreated quickly in recent years. In 2017, we surveyed the cold-adapted fungi in these unique habitats and obtained 1208 fungal strains. Based on preliminary analysis of ITS sequences, 41 isolates belonging to the genus *Cadophora* were detected. As one of the most frequently encountered genera, the *Cadophora* isolates were studied in detail. Two phylogenetic trees were constructed: one was based on the partial large subunit nrDNA (LSU) to infer taxonomic placement of our isolates and the other was based on multi-locus sequences of LSU, ITS, TUB and TEF-1 α to investigate more exact phylogenetic relationships of *Cadophora* and allied genera. Combined with morphological characteristics, nine *Cadophora* species were determined, including seven new to science. Among the new species, only *C. inflata* produced holoblastic conidia and all the others had phialidic conidiogenesis, and some isolates recognized as *C. qinghai-tibetana* and *C. psychrophila* had optimum growth temperature at 15°C. With more species involved, the currently circumscribed genus became obviously paraphyletic and all members clustered into two main clades: one clade mainly included most of the *Cadophora* species which had phialidic conidiogenesis and we referred to as '*Cadophora* s. str. '; the rest *Cadophora* species had multiform conidiogenesis and clustered in the second clade, with members of other genera in Ploettnerulaceae interspersed among the subclades. Our results showed a high diversity of *Cadophora* from marine glaciers in the Qinghai-Tibet Plateau and further intense sampling should be necessary for exploring more new species to reconstruct the phylogeny of this important fungal group.

Introduction

The genus *Cadophora* was first established in 1927, designating *C. fastigiata* as the type to accommodate dematiaceous hyphomycetes producing solitary phialides with distinct hyaline collarettes (Lagerberg et al. 1927). Due to subtle differences in morphology, Conant (1937) transferred eight *Cadophora* species to the highly polyphyletic genus *Phialophora*. Later, Gams (2000) proposed that *Phialophora* species related to discomycete teleomorphs of *Mollisia* and related genera belonging to the Helotiales should be accommodated in *Cadophora*. This decision was supported by subsequent rDNA sequence analysis of LSU (Harrington & McNew 2003).

Currently, the genus is included in the family Ploettnerulaceae of Helotiales (Johnston et al. 2019, Ekanayaka et al. 2019) and comprises some species with multiform morphological characters deviated from the original morphological generic concept. E. g. *C. orchidicola* forms sessile conidia laterally or sympodially on undifferentiated hyphae or short swollen conidiogenous cells (Currah et al. 1987); *C. antarctica*, *C. fascicularis* and *C. variabilis* produce chains of ramoconidia and conidia on holoblastic conidiogenous cells (Crous et al. 2017, Maciá-Vicente et al. 2020); while *C. obovata* have putatively monoblastic conidiogenous cells that may represent a retrogression of enteroblastic phialidic conidiogenesis and *C. fallopiae* was only observed a cladophialophora-like synasexual morph in culture (Maciá-Vicente et al. 2020, Crous et al. 2020). Besides, *C. lacrimiformis* with only sexual morph found was also included in this anamorphic genus (Ekanayaka et al. 2019). Recent studies based on molecular data have shown that *Cadophora* is apparently paraphyletic and species with distinct morphological variations may share ancestor with other related genera (Maciá-Vicente et al. 2020).

Species of *Cadophora* normally possess multiple trophic modes and they are commonly considered as plant pathogens, root associates, wood or soil colonizers with cosmopolitan distribution. Global survey on the dominant soil fungal communities of different biomes showed that *Cadophora* is one of the most ubiquitous soil fungal taxa with significantly higher number of genes related to stress-tolerance and resource uptake (Egidi et al. 2019). In some cold Arctic and Antarctic sites, *Cadophora* species have been frequently isolated from soils, marine sediments and organisms, fresh water lakes, especially the historic wood huts and some mummified or submerged drift wood (Blanchette et al. 2004, 2010, 2016, Jurgens et al. 2009, Goncalves et al. 2012, Furbino et al. 2014, Zhang et al. 2017, Nagano et al. 2017, Duran et al. 2019). They are hypothesized to be key organisms capable of initiating nutrient cycles and energy flows from dead organic materials in the high latitudes (Blanchette et al. 2016). Meanwhile, the saprotrophic species, mainly *C. malorum*, *C. luteo-olivacea*, and *C. fastigiata* which were frequently isolated from polar regions were also detected as pathogens or endophytes from different living plants worldwide (Di Marco et al. 2004, Gramaje et al. 2011, Navarrete et al. 2011, Travadon et al. 2015). Enzyme tests of some *Cadophora* members showed that *C. luteo-olivacea* and *C. malorum* were capable of degrading a range of carbon sources and releasing soluble phosphorus so that their trophic modes could vary depending on their nutrient needs from different substrata (Day & Currah 2011, Walsh et al. 2018).

The Qinghai-Tibet Plateau, lying across the center of Asia and having an average elevation of 4000 meters, possesses large number of glacial groups that constitute the center of Asian Highland Glaciers. According to Shi et al. (2000), glaciers in the Qinghai-Tibet Plateau can be divided into continental glaciers and marine glaciers. Controlled by the monsoonal climate, nearly 9000 marine glaciers with the features of fast accumulation and melting, more sensitive to the change of climate, form at the southeast range of Qinghai-Tibet Plateau

and cover a total area of 13200 square kilometers. Under the background of global warming, glaciers all over the world are retreating significantly. In the next 100 years, marine glaciers in the Qinghai-Tibet Plateau will retreat more quickly (Yao et al. 2004, Chen et al. 2005). It is necessary and urgent to investigate fungal diversity and resources in this unique area.

Our first investigation (2009–2011) on cold-adapted fungi in the permafrost and alpine glaciers of Qinghai-Tibet Plateau indicated that the diversity of cold-adapted fungi from marine glaciers is especially high and many of them may represent unknown species (Wang et al. 2015). Another survey was conducted in 2017, focusing on the diversity of cold-adapted fungi from marine glaciers. Based on preliminary analyses of the generated ITS sequences, 41 strains representing nine *Cadophora* species including seven new species were described and phylogenetic relationships among *Cadophora* and related genera were also discussed in this study.

Materials And Methods

Sample collection

Soil, ice and water samples were collected from four marine glaciers and two nearby snow mountains in 2017 (Table 1). Sampling sites were selected at different elevations of the following marine glaciers and snow mountains: Hailuogou Glacier, Yanzigou Glacier and Dagu Glacier in Sichuan Province, Yulong Snow Mountain, Baima Snow Mountain and Mingyong Glacier in Yunnan Province (Fig. 1, Fig. 2). For all samplings, clean hand tools were surface sterilized with 70% ethanol before use. After the removal of the top 5–10 cm of surface sediment, c. 500 g soil or ice sample was collected from the underlying layer and placed in a fresh Zip-lock plastic bag and sterilized plastic bottles. Melt water samples were directly collected and placed in sterilized centrifuge tubes or Zip-lock plastic bags. All the samples were maintained at 4°C until arrival at the laboratory.

Table 1
Collection details of samples from which *Cadophora* strains were isolated

Sampling location	Collection date	GPS location	Altitude (m)	Substrate
Baima Snow Mountain	10 May 2017	N28°23'29" E98°59'22"	4124.7	soil
		N28°22'59" E99°0'31"	4343	soil
		N29°23'1" E99°0'20"	4366.2	soil
Dagu Glacier	1 May 2017	N32°8'19" E102°56'13"	2380	soil
		N32°8'19" E102°56'13"	2380	water
		N32°15'38" E102°48'15"	3510	soil
		N32°14'23" E102°47'7"	3610	water
		N32°14'21" E102°47'5"	3630	soil
		N32°13'14" E102°45'29"	4850	soil
Hailuogou Glacier	28 April 2017	N29°33'10" E101°58'10"	3180	water
		N29°34'8" E101°59'36"	3180	soil
Mingyong Glacier	9 May 2017	N28°27'25" E98°45'51"	2960	water
		N28°27'24" E98°45'51"	2976	soil
		N28°27'27" E98°45'49"	2976	soil
		N28°27'28" E98°45'43"	3067	soil
Yanzigou Glacier	29 April 2017	N29°41'58" E102°0'7"	2620	soil
Yulong Snow Mountain	7 May 2017	N27°11'17" E100°22'43"	3362	soil
		N27°11'17" E100°22'43"	3362	water
		N27°10'52" E100°19'84"	4531	soil
		N27°10'55" E100°19'87"	4531	soil

Isolation and temperature selection

Strains were isolated from soil and water samples as soon as they were taken to the lab. Soil samples were isolated with traditional pour plate method: A 10 g quantity of each soil sample was suspended in sterile-distilled water in a flask, the volume was then increased to 100 mL before the suspension was shaken to disperse soil particles and then serially diluted to 10^{-2} , 10^{-3} and 10^{-4} ; 100 ml of each water sample was filtrated by nitrocellulose filter membrane with pore size of 0.45 μm , then put the membrane with trapped fungi in a sterile 50 ml centrifuge tube, added 10 ml distilled water and agitated the tube vigorously to suspend the trapped mycelium and spores. For the selection of psychrophilic and psychrotolerant fungi, about 0.1 mL of each final diluent or concentrate was placed on the surface of two 90 mm diam Petri plates containing 1/4 PDA (potato dextrose agar plus chloramphenicol at 0.1 mg/mL and streptomycin at 0.1 mg/mL to suppress bacterial growth) and spread evenly. The plates were sealed and incubated at 15°C and 25°C (one plate per temperature). The plates were examined for fungal growth at 1 wk intervals for 4 wk. Colonies that appeared on the plates were transferred to two new plates and then incubated at 15°C and 25°C as temperature test. The change in colony diameter after 2 wk (growth rate) was determined for each isolate at the two temperatures. The psychrophilic and psychrotolerant fungi isolated in this study were consolidated but not strictly in accordance with the definition given by Morita (1975), because the definition is very artificial and may not be applicable for most of the eukaryotes which may have much broader growth-temperature ranges. Fungi grew better at 15°C than that at 25°C and those grew better at 25°C were considered psychrophilic and psychrotolerant, respectively. The ex-type specimens were deposited in HBU (Mycological Herbarium of Hebei University) and the culture in CGMCC (China General Microbiological Culture Collection Center).

Morphological observations

41 isolates representing all of the *Cadophora* species isolated were studied in more detail. To enhance sporulation, strains were inoculated on potato dextrose agar (PDA; BD Difco), 2% malt extract agar (MEA, BD Difco) and oatmeal agar (OA; BD Difco). Pine needle medium, H_2O_2 treatment and slide culture technique (Xu et al. 2009, Su et al. 2012) were also used to induce sporulation. Cultures were incubated at 15°C and 25°C with three replicates. The colony diameter of fungi growing on PDA, MEA and OA plates were measured in two perpendicular directions after 2 wk at different temperatures, and the mean diameter was obtained from three replicate plates cultivated at the same temperatures. Colony colors were determined using taxonomic description color charts (Rayner 1970). Microscopic preparations were made by mounting aerial hyphae in water or using the slide cultures directly. Hyphae, conidiophores, and conidia were observed, photographed, and measured with 1000 $\times$ magnification by using a Nikon 80i microscope with differential interference contrast (DIC) optics.

DNA extraction, PCR amplification, sequencing and phylogenetic analyses

Genomic DNA was extracted from the fungal mycelia following the protocol described by Wang & Zhuang (2004). The partial large subunit nrDNA (LSU), the internal transcribed spacer region of the nuclear ribosomal RNA gene (ITS), the partial translation elongation factor 1- α gene (TEF-1 α) and the β -tubulin (β -TUB) gene were amplified and sequenced with the primer pairs of LROR/LR5 (Vilgalys & Hester 1990), ITS1/ITS4 (White et al. 1990), EF1-688F/EF1-1251R (Alves et al. 2008) and BTCadF/R (Travadon et al. 2015), respectively. PCR was performed in 50 μL reactions containing DNA template 1.0 μL , each forward and reverse primers 1.0 μL , 2 $\times$ MasterMix 25 μL (ThermoFisher scientific Co. Ltd., Shanghai, China) and 22 μL H_2O , using the following parameters: 95°C for 30 s; followed by 35 cycles at 54°C for LSU, 54°C for ITS, 51°C for TEF-1 α and 56°C for β -TUB gene for 30 s and 72°C for 60 s; and a final extension at 72°C for 7 min. The PCR products were sequenced with primers mentioned above by BGI Tech Solutions Co., Ltd. (Shenzhen, China).

Sequences were compared to accessions in the GenBank database via BLASTn searching to find the most likely taxonomic designation. To reveal the family placements of the species described in this paper, a LSU tree was constructed. To investigate more exact phylogenetic relationships and taxonomic distinctions of novel species, a multi-locus analysis was performed based on ITS, LSU, TUB and TEF1- α genes. Sequence data of the four genes especially those of ex-type strains, were downloaded from GenBank and added to the sequences generated in this study. The datasets were aligned automatically using MAFFT v. 7.471 (Katoh & Standley 2013) and further manual alignment was carried out with MEGA v. 7 (Kumar et al. 2016) and alignments were deposited in TreeBASE (www.treebase.org, submission no. S29383).

Phylogenetic analyses were conducted using Bayesian Inference (BI), Maximum Likelihood (ML) and Maximum Parsimony (MP) methods. For BI analyses, the best fit model of evolution for each partition was estimated by MEGA v. 7. Posterior probabilities were determined by Markov Chain Monte Carlo sampling (MCMC) in MrBayes v. 3.2.7a (Ronquist & Huelsenbeck 2003) using the estimated models of evolution. For the LSU/multi-locus trees, six simultaneous Markov chains were run for 4000 000/8 000 000 generations and trees were sampled every 100th generation (resulting in 40 000/80 000 total trees). The first 10 000/20 000 trees represented the burn-in phase of the analyses were discarded and the remaining 30 000/60 000 trees were used for posterior probabilities (PP) calculation in the majority rule

consensus trees. The ML analyses were performed by raxml GUI 2.0.0-beta (Edler et al. 2019) using the GTRGAMMA model with the rapid bootstrapping and search for best scoring ML tree algorithm, including 1000 bootstrap replicates. The MP analyses were conducted using PAUP v. 4.0b10 (Swofford 2002) and an unweighted parsimony (UP) analysis was performed. Trees were inferred using the heuristic search option with TBR branch swapping and 1 000 random sequence additions. Branches of zero length were collapsed and all equally most parsimonious trees were saved. Descriptive tree statistics such as tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI), were calculated for trees generated. Clade stability was assessed using bootstrap analysis with 1000 replicates, each with 10 replicates of random stepwise addition of taxa.

Results

1208 fungal strains isolated from 120 samples of four glaciers and two snow mountains were preliminarily identified based on BLAST comparison of ITS sequences against the GenBank database. As one of the most commonly encountered fungal groups, 41 isolates belonging to *Cadophora* were studied in detail.

Phylogenetic analyses

Sequences of referential species, especially those of ex-type strains, were retrieved from GenBank and added to the sequences generated in this study (Table 2). The alignments of partial sequences of LSU, ITS, LSU, TUB and TEF1- α have 855, 446, 828, 567, 693 characters respectively.

Table 2
Strains analyzed in this study, with collection details and GenBank accession numbers

Species	Strain no.	Host/ substrate	Country	GenBank Accession No.			
				LSU	ITS	TUB	TEF1- α
<i>Articulospora tetracladia</i>	DSM 104345	–	–	MK226456	MH930816	MK241460	MK241447
<i>Ascocorticium anomalum</i>	CBS 874.71	–	Germany	MH872135	–	–	–
<i>Cadophora anfricana</i>	CBS 120890 ^T	<i>Prunus salicina</i> , necrotic wood	South Africa	MT156170	MN232936	MN232967	MN232988
<i>Cadophora antarctica</i>	FMR16056 ^T	diesel-contaminated soil sample	Antarctica	MG385663	MG385664	–	–
<i>Cadophora bubakii</i>	CBS 198.30 ^T	margarine	Czech Republic	MH866559	MH855111	–	MN232989
<i>Cadophora caespitosa</i>	CGMCC3.20179 = MY156 ^T	water in Mingyong Glacier	China	MT908194	MT889936	MT921201	MT900568
<i>Cadophora caespitosa</i>	CGMCC3.20180 = MY169	water in Mingyong Glacier	China	MT908195	MT889937	MT921202	MT921172
<i>Cadophora caespitosa</i>	CGMCC3.20192 = DG1120	water in Dagu Glacier	China	MT908222	MT889964	MT921229	MT921197
<i>Cadophora caespitosa</i>	CGMCC3.20431 = HL674	water in Hailuoguo Glacier	China	MW793546	MW793520	MW818434	MW810619
<i>Cadophora caespitosa</i>	CGMCC3.20432 = BM691	soil in Baima Snow Mountain	China	MW793547	MW793521	MW818435	MW810620
<i>Cadophora constrictospora</i>	P1751 ^T	endophytic in roots of <i>Microthlaspi</i>	Bulgaria	MN339369	KT269023	–	MN325874
<i>Cadophora dextrinospora</i>	AG5	decayed wood in <i>Anoplophora glabripennis</i> galleries	Finland	–	MF188986	–	–
<i>Cadophora dextrinospora</i>	CBS 401.78 ^T	decaying wood	Spain	MH872917	NR_119489	–	–
<i>Cadophora echinata</i>	P6045 ^T	endophytic in roots of <i>Microthlaspi perfoliatum</i>	Spain	MN339428	KT270239	–	MN325932
<i>Cadophora fallopiae</i>	CPC 35742	Reynoutria japonica	Germany	MT223877	MT223782	–	–
<i>Cadophora fascicularis</i>	P2794 ^T	endophytic in roots of <i>Microthlaspi erraticum</i>	Germany	MN339414	KT269992	–	MN325918
<i>Cadophora fastigiata</i>	CBS 307.49	Pine wood	Sweden	MH868062	MH856538	KM497131	KM497087

^Tex-type strain; ¹LSU: large subunit nrDNA; ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; TUB: partial beta-tubulin gene; TEF1- α : partial translation elongation factor 1-alpha gene.

Species	Strain no.	Host/ substrate	Country	GenBank Accession No.			
				LSU	ITS	TUB	TEF1- α
<i>Cadophora ferruginea</i>	P1323 ^T	endophytic in roots of <i>Microthlaspi perfoliatum</i>	Spain	MN339356	KT268618	–	MN325861
<i>Cadophora gamsii</i>	P2437 ^T	endophytic in roots of <i>Microthlaspi erraticum</i>	France	–	KT269668	–	MN325899
<i>Cadophora gregata</i>	ATCC 11073 ^T	<i>Glycine max</i> , brown stem rot	Japan	MF979571	U66731	MF677920	MF979586
<i>Cadophora helianthi</i>	CBS 144752 ^T	<i>Helianthus annuus</i> , necrotic tissue in stem	Ukraine	–	MK813837	MH733391	MH719029
<i>Cadophora indistincta</i>	CGMCC3.20233 = DG978	soil in Dagū Glacier	China	MT908210	MT889952	MT921217	MT921186
<i>Cadophora indistincta</i>	CGMCC3.20234 = DG1054	water in Dagū Glacier	China	MT908215	MT889957	MT921222	MT921191
<i>Cadophora indistincta</i>	CGMCC3.20189 = DG1014 ^T	water in Dagū Glacier	China	MT908211	MT889953	MT921218	MT921187
<i>Cadophora indistincta</i>	CGMCC3.20195 = DG1017	soil in Dagū Glacier	China	MT908212	MT889954	MT921219	MT921188
<i>Cadophora indistincta</i>	CGMCC3.20196 = DG1074	soil in Dagū Glacier	China	MT908219	MT889961	MT921226	MT921194
<i>Cadophora inflata</i>	CGMCC3.20186 = MY759 ^T	soil in Mingyong Glacier	China	MT908204	MT889946	MT921211	MT921181
<i>Cadophora interclivum</i>	CBS143323 = BAG4 ^T	<i>Carex sprengelii</i> , root	Canada	MF979565	MF979577	MF677917	MF979583
<i>Cadophora lacrimiformis</i>	MFLU 16-1486 ^T	unknown Brassicaceae, dead stem	Russia	MK591959	MK585003	–	–
<i>Cadophora luteo-olivacea</i>	CBS 141.41 ^T	waste water	Sweden	MH867586	MH856092	KM497133	JN808856
<i>Cadophora luteo-olivacea</i>	GLMC 517	<i>Prunus domestica</i> , necrotic wood	Germany	–	MN232937	MN232968	MN233003
<i>Cadophora magna</i>	CGMCC3.20188 = MY902 ^T	soil in Mingyong Glacier	China	MT908208	MT889950	MT921215	MT921184
<i>Cadophora malorum</i>	CBS 165.42	<i>Amblystoma mexicanum</i>	Netherlands	MH867607	MH856109	KM497134	KM497090
<i>Cadophora malorum</i>	CGMCC3.20184 = YL412	soil in Yulong Snow Mountain	China	MT908200	MT889942	MT921207	MT921177
<i>Cadophora margaritata</i>	CBS 144084	Colonized wood	Finland	–	MH203866	–	–

^Tex-type strain; ¹LSU: large subunit nrDNA; ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; TUB: partial beta-tubulin gene; TEF1- α : partial translation elongation factor 1-alpha gene.

Species	Strain no.	Host/ substrate	Country	GenBank Accession No.			
				LSU	ITS	TUB	TEF1- α
<i>Cadophora margaritata</i>	CBS144083 ^T	Colonized wood	Finland	MH267288	KJ702027	MH327786	–
<i>Cadophora melinii</i>	CBS 268.33 ^T	probably wood-pulp	Sweden	MH866887	NR_111150	KM497132	KM497088
<i>Cadophora melinii</i>	ONC1	<i>Vitis vinifera</i> 'Cabernet Franc', wood canker	Canada	–	KM497033	KM497114	KM497070
<i>Cadophora melinii</i>	U11	<i>Vitis vinifera</i> 'Sangiovese', vascular discoloration	USA	–	KM497032	KM497113	KM497069
<i>Cadophora meredithiae</i>	CBS143322 = BAG2 ^T	<i>Carex sprengelii</i> , root	Canada	MF979568	MF979574	MF677914	MF979580
<i>Cadophora neoregeliae</i>	CBS 146821 ^T	from leaf spots of <i>Neoregelia</i> sp.	New Zealand	MZ064468	MZ064411	–	–
<i>Cadophora novi-eboraci</i>	GLMC 239	<i>Prunus cerasus</i> , necrotic wood	Germany	–	MN232942	MN232973	MN232990
<i>Cadophora novi-eboraci</i>	GLMC 273	<i>Prunus cerasus</i> , necrotic wood	Germany	MT156177	MN232943	MN232974	MN232991
<i>Cadophora novi-eboraci</i>	NYC14 ^T	<i>Vitis labruscana</i> , wood canker	USA	–	KM497037	KM497118	KM497074
<i>Cadophora novi-eboraci</i>	CGMCC3.20190 = YZ1034	soil in Yanzigou Glacier	China	MT908213	MT889955	MT921220	MT921189
<i>Cadophora novi-eboraci</i>	CGMCC3.20434 = YZ1026	soil in Yanzigou Glacier	China	MW793552	MW793526	MW818436	MW810622
<i>Cadophora obovata</i>	P1963 ^T	endophytic in roots of <i>Microthlaspi erraticum</i>	Germany	MN339384	KT269230	–	MN325888
<i>Cadophora orchidicola</i>	UAMH 8152	<i>Pedicularis bracteosa</i> , root	Canada	MF979572	AF214576	MF677921	MF979587
<i>Cadophora orientoamericana</i>	CTC5	<i>Vitis</i> hybrid 'Cayuga white', wood canker	USA	–	KM497015	KM497096	KM497052
<i>Cadophora orientoamericana</i>	MYA-4972 = NHC1 ^T	<i>Vitis vinifera</i> 'Niagara'	USA	MF979573	KM497018	KM497099	KM497055
<i>Cadophora prunicola</i>	CBS 120891 ^T	<i>Prunus salicina</i> , necrotic wood	South Africa	MT156182	MN232949	MN232979	MN232997

^Tex-type strain; ¹LSU: large subunit nrDNA; ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; TUB: partial beta-tubulin gene; TEF1- α : partial translation elongation factor 1-alpha gene.

Species	Strain no.	Host/ substrate	Country	GenBank Accession No.			
				LSU	ITS	TUB	TEF1- α
<i>Cadophora prunicola</i>	GLMC 276	<i>Prunus cerasus</i> , necrotic wood	Germany	–	MN232951	MN232980	MN232998
<i>Cadophora psychrophila</i>	CGMCC3.20845 = DG5	soil in Dagu Glacier	China	OL477357	OL477351	OL674144	OL674147
<i>Cadophora psychrophila</i>	CGMCC3.20846 = DG21 ^T	soil in Dagu Glacier	China	OL477356	OL714365	OL674143	OL674146
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20181 = BM327	soil in Baima Snow Mountain	China	MT908197	MT889939	MT921204	MT921174
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20182 = YL357	water in Yulong Snow Mountain	China	MT908198	MT889940	MT921205	MT921175
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20183 = BM360	soil in Baima Snow Mountain	China	MT908199	MT889941	MT921206	MT921176
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20185 = MY474	soil in Mingyong Glacier	China	MT908202	MT889944	MT921209	MT921179
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20191 = DG1048	soil in Dagu Glacier	China	MT908214	MT889956	MT921221	MT921190
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20193 = DG1156 ^T	soil in Dagu Glacier	China	MT908223	MT889965	MT921230	MT921198
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20194 = YL414	water in Yulong Snow Mountain	China	MT908201	MT889943	MT921208	MT921178
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20197 = DG1105	soil in Dagu Glacier	China	MT908221	MT889963	MT921228	MT921196
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20228 = YL73	soil in Yulong Snow Mountain	China	MT908193	MT889905	MT921200	MT898424
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20229 = YL319	water in Yulong Snow Mountain	China	MT908196	MT889938	MT921203	MT921173
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20230 = BM523	soil in Baima Snow Mountain	China	MT908203	MT889945	MT921210	MT921180
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20231 = MY873	soil in Mingyong Glacier	China	MT908207	MT889949	MT921214	MT921183
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20232 = DG975	soil in Dagu Glacier	China	MT908209	MT889951	MT921216	MT921185
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20235 = DG1073	soil in Dagu Glacier	China	MT908218	MT889960	MT921225	MT921193
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20236 = DG1087	soil in Dagu Glacier	China	MT908220	MT889962	MT921227	MT921195
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20433 = BM857	soil in Baima Snow Mountain	China	MW793551	MW793525	MW818439	MW810621

^Tex-type strain; ¹LSU: large subunit nrDNA; ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; TUB: partial beta-tubulin gene; TEF1- α : partial translation elongation factor 1-alpha gene.

Species	Strain no.	Host/ substrate	Country	GenBank Accession No.			
				LSU	ITS	TUB	TEF1- α
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20435 = YL305	water in Yulong Snow Mountain	China	MW793548	MW793522	MW818433	–
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20436 = BM816	soil in Baima Snow Mountain	China	MW793550	MW793524	MW818438	–
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20437 = HL876	soil in Hailuoguo Glacier	China	MW793549	MW793523	MW818437	–
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20847 = MY492	soil in Mingyong Glacier	China	OL477358	OL477352	OL674145	OL674148
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20848 = MY527	soil in Mingyong Glacier	China	OL815016	OL815013	OL790381	OL790384
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20849 = MY588	soil in Mingyong Glacier	China	OL815017	OL815014	OL790382	OL790385
<i>Cadophora qinghai-tibetana</i>	CGMCC3.20850 = MY589	soil in Mingyong Glacier	China	OL815018	OL815015	OL790383	OL790386
<i>Cadophora ramosa</i>	CBS 111743	<i>Actinidia chinensis</i> , vascular discoloration	Italy	–	DQ404351	KM497136	KM497091
<i>Cadophora ramosa</i>	GLMC 377 ^T	<i>Prunus cerasus</i> , necrotic wood	Germany	MT156187	MN232956	MN232984	MN233002
<i>Cadophora sabaouae</i>	WAMC117	<i>Vitis vinifera</i>	Algeria	–	MT524745	MT646750	MT646747
<i>Cadophora sabaouae</i>	WAMC118	<i>Vitis vinifera</i>	Algeria	–	MT524744	MT646751	MT646748
<i>Cadophora sabaouae</i>	WAMC34 ^T	<i>Vitis vinifera</i>	Algeria	–	MT644187	MT646749	MT646746
<i>Cadophora variabilis</i>	P1176 ^T	endophytic in roots of <i>Microthlaspi perfoliatum</i>	Croatia	MK539845	KT268493	–	MK550890
<i>Cadophora viticola</i>	Cme-1	<i>Vitis vinifera</i> 'Syrah', black streaks in shoots	Spain	–	HQ661096	HQ661096	HQ661081
<i>Cadophora viticola</i>	Cme-2 ^T	<i>Vitis vinifera</i> 'Syrah', black streaks in shoots	Spain	–	HQ661097	HQ661097	HQ661082
<i>Cadophora yulongensis</i>	CGMCC3.20187 = YL814 ^T	soil sample in Yulong Snow Mountain	China	MT908206	MT889948	MT921213	MT921182
<i>Calycina alstrupii</i>	Pz162 ^T	on <i>Lobaria pulmonaria</i> growing on trunk of <i>Alnus incana</i>	Norway	KY305097	–	–	–

^Tex-type strain; ¹LSU: large subunit nrDNA; ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; TUB: partial beta-tubulin gene; TEF1- α : partial translation elongation factor 1-alpha gene.

Species	Strain no.	Host/ substrate	Country	GenBank Accession No.			
				LSU	ITS	TUB	TEF1- α
<i>Calycina marina</i>	TROM F26093	dead seaweed (<i>Ascophyllum nodosum</i>)	Norway	KT185670	–	–	–
<i>Cenangium acuum</i>	TAAM 198449	<i>Pinus sylvestris</i>	Czech Republic	KX090828	–	–	–
<i>Cenangium ferruginosum</i>	CBS 556.70	–	Netherlands	MH871625	–	–	–
<i>Cephalosporium gramineum</i>	CBS 132.34 ^T	<i>Triticum aestivum</i> , culm	Japan	NG_070839	NR_171209	–	–
<i>Chaetomella acutiseta</i>	AFTOL-ID 270	–	–	AY544679	–	–	–
<i>Chaetomella oblonga</i>	CBS 110.78	leaf of <i>Acer</i> sp.	Canada	MH872875	–	–	–
<i>Chlorociboria aeruginosa</i>	CBS 139.28	–	–	MH877688	–	–	–
<i>Chlorociboria clavula</i>	D1611	–	New Zealand	JN939941	–	–	–
<i>Collembolispora aristata</i>	CPC21145 ^T	foam in an unnamed right tributary of the brook Bezenek	Czech Republic	KC005811	NR_111830	–	KC005818
<i>Collembolispora barbata</i>	CBS 115944 = UMB-088.01 ^T	mountain freshwater stream	Portugal		NR_111443	–	–
<i>Cordierites frondosa</i>	HKAS41508	–	–	AY789354	–	–	–
<i>Cordierites guianensis</i>	192	–	–	EU107270	–	–	–
<i>Cudoniella clavus</i>	AFTOL-ID 166	–	–	DQ470944	–	–	–
<i>Dermea bicolor</i>	CBS 135.46	–	Canada	MH867659	–	–	–
<i>Dermea cerasi</i>	CBS 432.67	–	–	MH870721	–	–	–
<i>Graphium rubrum</i>	CBS 210.34 ^T	–	USA	MH866974	–	–	–
<i>Helgardia anguioides</i>	CBS 496.80 ^T	–	Germany	MH873055	–	–	–
<i>Helgardia anguioides</i>	RAN45	–	Germany	–	AY266144	–	–
<i>Hyaloscypha finlandica</i>	CBS 444.86 ^T	<i>Pinus sylvestris</i> , root of seedling	Finland	MH873675	NR_121279	KM497130	KM497086
<i>Hyaloscypha melinii</i>	CBS 143705 ^T	–	Czech Republic	NG_068558	–	–	–
<i>Hyaloscypha vitreola</i>	CBS 126276	–	Finland	MH875413	–	–	–
<i>Lachnum carneolum</i>	CBS 231.54	–	France	MH868838	–	–	–
<i>Lachnum diminutum</i>	CBS 232.54	–	France	MH868839	–	–	–

^Tex-type strain; ¹LSU: large subunit nrDNA; ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; TUB: partial beta-tubulin gene; TEF1- α : partial translation elongation factor 1-alpha gene.

Species	Strain no.	Host/ substrate	Country	GenBank Accession No.			
				LSU	ITS	TUB	TEF1- α
<i>Leotia lubrica</i>	KKM 427	mycorrhizal root tip	Costa Rica	KF836631	–	–	–
<i>Mastigosporium album</i>	CPC 22945 ^T	<i>Alopecurus pratensis</i>	Netherlands	KJ710451	KJ710476	–	–
<i>Mastigosporium kitzebergense</i>	CBS 270.69 ^T	–	Germany	MH871040	MH859306	–	–
<i>Mollisia cinerea</i>	CBS 122029	fallen log	USA	MT026558	–	–	–
<i>Mollisia cinerella</i>	CBS 312.61	–	France	MH869631	MH858062	–	–
<i>Mollisia discolor</i>	CBS 289.59	–	France	MT026504	–	–	–
<i>Mollisia fallens</i>	CBS 221.56	–	Netherlands	MT026505	–	–	–
<i>Mycochaetophora gentianae</i>	MAFF 239231 ^T	–	Japan	AB496937	NR_121201	–	–
<i>Mycochaetophora</i> sp.	MAFF 239284	–	Japan	AB469680	AB469681	–	–
<i>Neospermospora avenae</i>	CBS 227.38 ^T	<i>Avena sativa</i>	USA	NG_077377	MW298276	–	–
<i>Oculimacula acuformis</i>	CBS 495.80 ^T	culm base	Germany	MH873054	MH861289	–	MG934497
<i>Oculimacula aestiva</i>	CBS 114730	–	Sweden	–	MG934454	–	MG934496
<i>Oculimacula yallundae</i>	CBS 128.31	–	France	–	MH855154	–	MG934499
<i>Oculimacula yallundae</i>	CBS 494.80	culm base	Germany	–	JF412009	–	MG934500
<i>Phialocephala dimorphospora</i>	CBS 976.72	–	Germany	MH878299	–	–	–
<i>Phialophora dancoi</i>	CBS 329.90 ^T	–	Argentina	MH873899	MH862214	–	–
<i>Pleuroascus nicholsonii</i>	CBS 345.73 ^T	the dung of pack rat	USA	MH872404	–	–	–
<i>Porodiplodia livistoniae</i>	CPC 32154 ^T	<i>Livistona australis</i>	Australia	NG_069575	–	–	–
<i>Porodiplodia vitis</i>	CBS 144634 ^T	<i>Vitis vinifera</i>	USA	MK442552	–	–	–
<i>Rhexocercosporidium camporesii</i>	MFLU 17-1594 ^T	dead stems	Italy	MN688632	MN688634	–	–
<i>Rhexocercosporidium carotae</i>	CBS 418.65 ^T	–	Norway	MH870289	NR_111086	–	–
<i>Rhexocercosporidium microsporum</i>	MFLU 18-2672 ^T	unknown Apiaceae, stem	UK	MK591966	MK584939	–	–
<i>Rhynchosporium agropyri</i>	H11	–	–	–	HM627478	–	HM627463
<i>Rhynchosporium commune</i>	H7	–	–	–	–	HM627434	HM627459
<i>Rhynchosporium commune</i>	H10	–	–	–	–	HM627437	HM627462

^Tex-type strain; ¹LSU: large subunit nrDNA; ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; TUB: partial beta-tubulin gene; TEF1- α : partial translation elongation factor 1-alpha gene.

Species	Strain no.	Host/ substrate	Country	GenBank Accession No.			
				LSU	ITS	TUB	TEF1- α
<i>Rhynchosporium orthosporum</i>	04CH-Bar-A.1.1.3	<i>Dactylis glomerata</i>	Switzerland	KU844335	–	–	–
<i>Rhynchosporium secalis</i>	02CH4-6a.1	–	Switzerland	–	KU844333	–	–
<i>Rutstroemia bulgarioides</i>	TAAM 198322	fallen cone	Estonia	KX090836	–	–	–
<i>Rutstroemia firma</i>	CBS 115.86 ^T	–	Netherlands	MH873619	–	–	–
<i>Sclerotinia bulborum</i>	CBS 297.31	–	USA	MH866668	–	–	–
<i>Sclerotinia sclerotiorum</i>	WZ0067	–	China	AY789347	–	–	–
<i>Xylaria hypoxylon</i>	CBS 120.16	–	–	MH866173	–	–	–
<i>Ypsilina buttingtonensis</i>	CPC 39109 ^T	from heartwood of 1000-yr-old <i>Quercus</i> sp.	UK	MT373355	MT373372	–	–
<i>Ypsilina graminea</i>	CBS 114630 ^T	–	UK	MH874529	NR_160217	–	–
^T ex-type strain; ¹ LSU: large subunit nrDNA; ITS: Internal transcribed spacers 1 and 2 together with 5.8S nrDNA; TUB: partial beta-tubulin gene; TEF1- α : partial translation elongation factor 1-alpha gene.							

According to the LSU phylogenetic tree, representative *Cadophora* strains of this study (marked with bold font) and the known *Cadophora* species were interspersed with species of other genera in Ploettnerulaceae and formed a well-supported clade (BP/BP/PP = 90/98/100, ML/MP bootstrap and BI posterior probability support values, respectively) that distinctly separated from other family members in the Helotiales (Fig. 3).

A multi-gene phylogenetic tree was also employed to investigate further phylogenetic relationships intra and among *Cadophora* and allied genera (Fig. 4). All the representative species clustered into two main clades with high ML/MP bootstrap or BI posterior probability support values (92/80/100, 97/-/100 respectively). In the first main clade (Clade1), 38 isolates of this study formed six distinct subclades: isolates of YZ1026 and YZ1034 clustered in a lineage including the ex-type sequences of *C. novi-eboraci* with strong branch support; although strain MY902 and the known species of *Cephalosporium greminum* formed a well supported subclade, they were obviously distinguished morphologically and the placement of *C. greminum* should also be confirmed by protein coding genes which were unavailable currently; the other four subclades grouped separately with previously described species. Combined with morphological characteristics, we proposed five *Cadophora* species new to science: *Cadophora caespitosa*, *C. indistincta*, *C. magna*, *C. psychrophila* and *C. qinghai-tibetana*. Clade 1 also included most of the phialidic *Cadophora* species (including the type) and three species (*Cephalosporium gramineum*, *Mollisia cinerella* and *Phialophora dancoi*) belonged to other genera. The second main clade (Clade 2) contained the rest *Cadophora* species and most other Ploettnerulaceae members. Three isolates of this study were included in this clade: strain YL412 clustered with *C. malorum* in a well supported lineage; strain MY759 and MY814 formed two distinct single strain clades and we proposed them as two new species (*Cadophora inflata* and *Cadophora yulongensis*). *Cadophora* species in Clade 2 had multiform conidiogenesis modes and formed lineages interspersed by other Ploettnerulaceae members.

Taxonomy

Cadophora caespitosa Q-M Wang, B-Q Zhang & M-M Wang, **sp. nov.**

Mycobank No.: MB837889.

Figure 5

Etymology

Referring to multiple phialides arranged in terminal fascicles.

Type: **China:** Yunnan Province, Mingyong Glacier, N28°27'25" E98°45'51", 2960 m, from water, 9 May 2017, M-M Wang, holotype HBU20001, culture ex-type MY156 = CGMCC3. 20179.

Mycelium hyaline to brown, septate, smooth-walled, branched, 1–3 µm wide. Conidiophores pale brown or hyaline, straight, septate, smooth, branched or unbranched, bearing solitary or multiple phialides. Conidiogenous cells phialidic, located laterally on fertile hyphae or arranged in complex heads, cylindrical to navicular, often constricted at the base, upper subulate, hyaline, smooth-walled, $6.49\text{--}32.32 \times 2.56\text{--}3.83$ µm, collarettes distinct, funnel-shaped, 1.92–3.89 µm long, opening 1.85–3.36 µm wide. Conidia hyaline, aseptate, smooth-walled, sporulation abundant, ovate to dacryoid or ellipsoidal, single, with both ends rounded, straight, $3.37\text{--}7.05 \times 1.71\text{--}3.41$ µm (mean = $5.02 \pm 0.85 \times 2.58 \pm 0.41$ µm, n = 30), L/W ratio = 1.95.

Culture characteristics — Colonies on MEA reaching 33 mm diam after 14 d at 25°C in the dark, on OA and PDA reaching 55 mm and 34 mm diam, respectively. Colonies on MEA with a smooth margin, flat, grey-white, buff to light yellow at the margin, reverse olive-black. Colonies on OA with an entire margin, flat, greenish-black with a white margin, reverse same colours. Colonies on PDA with an entire margin, flat, hazel to yellow-brown with a beige margin, reverse same colours.

Additional specimens examined: **China:** Sichuan Province, Dagu Glacier, N32°14'23" E 102°47'7", 3610 m, from water, 1 May 2017, M-M Wang, culture DG1120 = CGMCC3.20192; Sichuan Province, Hailuoguo Glacier, N29°33'10" E101°58'10", 3180 m, from water, 28 Apr. 2017, M-M Wang, culture HL674 = CGMCC3.20431; Yunnan Province, Baima Snow Mountain, N28°23'29" E98°59'22", 4124.7 m, from soil, 10 May 2017, M-M Wang, BM691 = CGMCC3.20432; Yunnan Province, Mingyong Glacier, N28°27'25" E98°45'51", 2960 m, from water, 9 May 2017, M-M Wang, culture MY169 = CGMCC3.20180.

Notes — According to Day et al. (2012), the genera *Cadophora* and *Phialocephala* are generally distinguished by phialide complexity and conidial length, with the former producing solitary phialides and conidia longer than 4 µm, while the latter producing densely packed heads of phialides and conidia shorter than 4 µm. The newly described species is characterized by having distinct, dark stipe with multiple phialides terminating in a complexly penicillately branched apex. Phylogenetic analyses based on sequences of LSU and combined ITS + LSU + TUB + TEF1-α regions clearly show that *C. caespitosa* grouped with species of *Cadophora* in the family of Ploettnerulaceae and formed a well supported lineage.

Cadophora indistincta Q-M Wang, B-Q Zhang & M-M Wang, **sp. nov.**

Mycobank No.: MB837895.

Figure 6

Etymology

Referring to the indistinct collarettes of phialides.

Type: **China:** Sichuan Province, Dagu Glacier, N32°8'19" E102°56'13", 2380 m, from water, 1 May 2017, M-M Wang, holotype HBU20012, culture ex-type DG1014 = CGMCC3.20189.

Mycelium hyaline, septate, smooth-walled, branched, 1–4 µm. Conidiophores hyaline, septate, smooth, often solitary. Conidiogenous cells phialidic, located terminally or laterally, discrete, hyaline, smooth-walled, straight or curved, cylindrical to navicular, often inflated in the middle and constricted at the base, $5.28\text{--}31.43 \times 1.57\text{--}3.69$ µm, collarettes indistinct, most phialides lack collarettes. Conidia hyaline, aseptate, smooth-walled, cylindrical to oblong, $4.67\text{--}7.50 \times 1.62\text{--}2.54$ µm (mean = $5.46 \pm 0.66 \times 2.17 \pm 0.23$ µm, n = 30), L/W ratio = 2.52.

Culture characteristics — Colonies on MEA reaching 45 mm diam, after 14 d at 25°C in the dark, on OA and PDA reaching 49 mm and 44 mm diam, respectively. Colonies on MEA flat, primrose to pale citrine, white at the margin, reverse same colours. Colonies on OA with a yellow margin, surface black-brown, aerial mycelium sparse, reverse same colours. Colonies on PDA with a distinct and smooth margin, flat, grayish to red, ivory at the edge, reverse darkred.

Additional specimens examined: **China:** Sichuan Province, Dagu Glacier, N32°8'19" E102°56'13", 2380 m, from soil, 1 May 2017, M-M Wang, culture DG978 = CGMCC3.20233; DG1074 = CGMCC3.20196; N32°15'38" E102°48'15", 3510 m, from soil, 1 May 2017, M-M Wang, culture DG1017 = CGMCC3.20195; N32°14'23" E102°47'7", 3610 m, from water, 1 May 2017, M-M Wang, culture DG1054 = CGMCC3.20234.

Notes — *Cadophora indistincta* has some similarities with *C. ferruginea*: red colour colonies on PDA and indistinct collarettes, but the two species are distinguished by conidia shapes: *C. indistincta* produces cylindrical to oblong conidia (L/W ratio = 2.52) while *C. ferruginea*

produces ellipsoidal conidia (L/W ratio = 1.8).

Cadophora inflata Q-M Wang, B-Q Zhang & M-M Wang, **sp. nov.**

MycoBank No.: MB837892.

Figure 7

Etymology

Referring to the characteristics of the inflated hyphae.

Type: **China:** Yunnan Province, Mingyong Glacier, N28°27'24" E98°45'51", 2976 m, from soil, 9 May 2017, M-M Wang, holotype HBU20009, culture ex-type MY759 = CGMCC3.20186.

Mycelium olivaceous or hyaline, septate, branched, smooth-walled, 2–4 µm wide. Hyphal cells often strongly inflated, up to 6–10 µm wide, form chains or microsclerotia-like bodies. Conidiophores always very short or invisible. Conidiogenous cells holoblastic. Conidia hyaline, attached to mycelium, located laterally or terminally, smooth-walled, globular or spathulate, solitary, 2.93–7.05 × 3.00–4.44 µm (mean = 3.91 ± 0.78 × 3.71 ± 0.42 µm, n = 30), L/W ratio = 1.05.

Culture characteristics — Colonies on MEA reaching 28 mm diam, after 14 d at 25°C in the dark, on OA and PDA reaching 47 mm and 37 mm diam, respectively. Colonies on MEA, with an entire margin, flat, milk-white, lacking aerial mycelium, reverse same colours. Colonies on OA with a smooth margin, flat, black in the center, olivaceous to white from middle to edge, reverse same colours. Colonies on PDA with a smooth margin, felty, grey, pale yellow at the margin, reverse grey-brown with a pale buff to white margin.

Notes — *Cadophora inflata* is characterized by producing chains or microsclerotia-like inflated cells that are similar to *C. gamsii* and *C. echinata* which were first described by Maciá-Vicente et al. (2020) and the authors supposed these structures as holoblastic conidia or may just be interpreted as inflated hyphal segments with dormancy functions. The newly described species failed to produce conidia at first, after being induced by slide culture technique, the isolate produced globose or ellipsoidal conidia attaching directly to the hyphae with very short conidiophores that resembled *Cadophora orchidicola* and thus we suppose that the inflated hyphal cells were just chlamydospores.

Cadophora magna Q-M Wang, B-Q Zhang & M-M Wang, **sp. nov.**

MycoBank No.: MB837893.

Figure 8

Etymology

Referring to the comparatively huge conidia.

Type: **China:** Yunnan Province, Mingyong Glacier, N28°27'24" E98°45'51", 2976 m, from soil, 9 May 2017, M-M Wang, holotype HBU20011, culture ex-type MY902 = CGMCC3.20188.

Mycelium hyaline to dark brown, septate, smooth-walled, 1–3 µm, hyphal cells often strongly inflated, variable in shape. Conidiophores brown, smooth-walled, often reduced to conidiogenous cells. Conidiogenous cells phialidic, mostly single, arranged terminally or laterally on the hyphae, cylindrical to navicular, apex wedge, base truncate, smooth-walled, straight or slightly curved, 12.69–20.28 × 2.81–3.84 µm, collarettes funnel-shaped, 1.93–2.98 µm long, opening 2.79–2.88 µm wide. Conidia hyaline, aseptate, smooth-walled, ovoidal or dacryoid to ellipsoidal, upper wedge-shaped, base round, single, straight, 5.24–9.36 × 3.02–4.71 µm (mean = 7.34 ± 0.93 × 3.73 ± 0.39 µm, n = 30), L/W ratio = 1.97.

Culture characteristics — Colonies on MEA reaching 30 mm diam after 14 d at 25°C in the dark, on OA and PDA reaching 41 mm and 29 mm diam, respectively. Colonies on MEA white, margin covered with ivory and velvety aerial mycelium, reverse white. Colonies on OA with a smooth margin, flat, whitish, pale olive in the centre, reverse same colours. Colonies on PDA creamy to white, reverse same colours.

Notes — The newly described species was isolated from soil samples of Mingyong Glacier and characterized by the huge conidia and strongly inflated hyphal cells.

Figure 9

Mycelium brown-black, septate, smooth-walled, branched, 2–3 µm. Conidiophores brown-black, septate, smooth. Conidiogenous cells phialidic, often forming clusters, terminally or laterally on the hyphae, smooth-walled, straight, ampulliform, often 9.47–15.97 × 2.87–3.47 µm, collarettes distinct, collarettes short tubular to funnel-shaped, 1.09–1.98 µm long, opening 1.62–1.94 µm wide. Conidia fuscous, aseptate, smooth-walled, ellipsoidal to elongate-ellipsoidal or subglobose, single, straight, 2.74–4.72 × 1.86–3.40 µm (mean = 3.70 ± 0.51 × 2.46 ± 0.35 µm, n = 30), L/W ratio = 1.50.

Culture characteristics — Colonies on MEA reaching 41 mm diam, after 14 d at 25°C in the dark, on OA and PDA reaching 60 mm and 48 mm diam, respectively. Colonies on MEA with a weakly undulate margin, brown-grey to yellow-brown, reverse same colours. Colonies on OA with a distinct and white margin, olivaceous to dull green, reverse same colours. Colonies on PDA with a distinct margin, felty, gray-brown to gray, reverse isabelline.

Specimen examined: **China**: Yunnan Province, Yulong Snow Mountain, N27°11'17" E100°22'43", 3362 m, from soil, 7 May 2017, M-M Wang, culture YL412 = CGMCC3.20184.

Notes — *Cadophora malorum* was the commonest *Cadophora* species and often isolated as saprobes or pathogens worldwide. Strain YL412 was isolated from soil samples collected from Yulong Snow Mountain and the morphological characteristics were similar with the type.

Cadophora novi-eboraci Travadon, D.P.Lawr., Roon.-Lath., Gubler, W.F. Wilcox, Rolsh. & K. Baumgartner

Figure 10

Mycelium hyaline to brown, septate, smooth-walled, branched, 1–3 µm. Conidiophores hyaline, aseptate, smooth, often solitary. Conidiogenous cells phialidic, terminally or laterally on the hyphae, discrete conidiogenous cells hyaline, smooth-walled, curved or straight, cylindrical to navicular, 6.22–19.90 × 2.38–3.04 µm, collarettes short, tubular, 0.97–1.93 µm long, opening 1.42–1.83 µm wide. Conidia hyaline, aseptate, smooth-walled, elongate-ellipsoidal to cylindrical, straight, 3.90–8.29 × 1.75–2.69 µm (mean = 5.81 ± 1.04 × 2.27 ± 0.26 µm, n = 30), L/W ratio = 2.56.

Culture characteristics — Colonies on MEA reaching 29 mm diam, after 14 d at 25°C in the dark, on OA and PDA reaching 26 mm and 28 mm diam, respectively. Colonies on MEA with an undulate margin, surface beige to ivory, reverse same colours. Colonies on OA with a distinct margin, flat, citrine to pure yellow, white at edge, reverse luteus. Colonies on PDA with a distinct margin, raised, beige to whitish, sometimes covered by floccose aerial mycelium, reverse same colours.

Specimens examined: **China**: Sichuan Province, Yanzigou Glacier, N29°41'58" E102°0'7", 2620 m, from soil, 29 Apr. 2017, M-M Wang, culture YZ1026 = CGMCC3.20434; YZ1034 = CGMCC3.20190.

Notes — *Cadophora novi-eboraci* was originally described from decaying wood of Grapevine in North America mainly based on phylogenetic analyses of three nuclear loci (ITS, BT and TEF1-α) (Travadon et al. 2015). Then it was also isolated from Prunus wood or freshwater (Bien & Dam 2020, Lim et al. 2021) and our strains were isolated from soil samples of Yanzigou Glacier in China.

Cadophora psychrophila Q-M Wang, B-Q Zhang & M-M Wang, **sp. nov.**

MycoBank No.: MB837890.

Figure 11

Etymology

Referring to cold loving.

Type: **China**: Sichuan Province, Dagu Glacier, N32°14'21" E102°47'5", 3630 m, from soil, 1 May 2017, M-M Wang, holotype HBU20040, culture ex-type DG21 = CGMCC3.20846.

Mycelium black brown or hyaline, septate, smooth-walled, branched, 1–3 µm. Mycelial cell occasionally inflated in the middle, up to 5–8 µm wide, constricted at the septate. Conidiophores black brown or hyaline, septate, mesotonously branched or unbranched. Conidiogenous

cells phialidic, hyaline, smooth-walled, tapering toward the tip and slightly constricted at the base, $13.43\text{--}23.50 \times 2.18\text{--}3.84 \mu\text{m}$, collarettes distinct and funnel-shaped, $2.82\text{--}4.78 \mu\text{m}$ long, opening $2.61\text{--}3.80 \mu\text{m}$ wide. Conidia hyaline, aseptate, smooth-walled, with subulate tip and round base, single, straight, $4.47\text{--}7.77 \times 2.09\text{--}3.18 \mu\text{m}$ (mean = $5.53 \pm 0.69 \times 2.67 \pm 0.34 \mu\text{m}$, $n = 30$), L/W ratio = 2.07.

Culture characteristics — Colonies on MEA reaching 19 mm diam, after 14 d at 15°C and 13 mm at 25°C in the dark, on OA reaching 28 mm at 15°C and 19 mm at 25°C , and on PDA reaching 25 mm at 15°C and attaining 17 mm at 25°C , respectively. Colonies on MEA raised, glabrous, citrine to primrose, reverse same colours. Colonies on OA with a smooth margin, flat, olive brown in the centre, whitish white at the margin, reverse same colours. Colonies on PDA with a whitish margin, slight raised, pure yellow, reverse same colours.

Additional specimens examined: **China:** Sichuan Province, Dagu Glacier, $\text{N}32^\circ14'21'' \text{E}102^\circ47'5''$, 3630 m, from soil, 1 May 2017, M-M Wang, culture DG5 = CGMCC3.20845.

Notes — *Cadophora psychrophila* was characterized by sparse aerial mycelium and slowly growing colony and both isolates in this study showed psychrophilic characteristics that their optimum growth temperature was 15°C .

Cadophora qinghai-tibetana Q-M Wang, B-Q Zhang & M-M Wang, **sp. nov.**

MycoBank No.: MB837896.

Figure 12

Etymology

Referring to geographical location from which the isolates collected.

Type: **China:** Sichuan Province, Dagu Glacier, $\text{N}32^\circ8'19'' \text{E}102^\circ56'13''$, 2380 m, from soil, 1 May 2017, M-M Wang, holotype HBU20019, culture ex-type DG1156 = CGMCC3.20193.

Mycelium hyaline or brown-black, septate, smooth-walled, branched, $2\text{--}4 \mu\text{m}$, often forming coils up to $34.88 \mu\text{m}$ diam. Conidiophores hyaline, smooth, frequently reduced to conidiogenous cells. Conidiogenous cell phialidic, laterally on the hyphae or hyphae coils, single or in groups of two or three, the mesotonously branched ones often reduced to mere openings with collarettes formed directly on conidiophores, cylindrical or navicular, inflated in the middle and attenuated at the base, hyaline or fuscous, smooth-walled, straight or curved, $6.82\text{--}19.94 \times 1.97\text{--}3.85 \mu\text{m}$, collarettes funnel-shaped or absence, $1.61\text{--}2.46 \mu\text{m}$ long, opening $1.57\text{--}2.72 \mu\text{m}$ wide. Sporulation abundant, conidia hyaline, aseptate, smooth-walled, cylindrical to elongate-ellipsoidal, $5.03\text{--}7.34 \times 1.74\text{--}2.72 \mu\text{m}$ (mean = $6.00 \pm 0.66 \times 2.13 \pm 0.21 \mu\text{m}$, $n = 30$), L/W ratio = 2.82.

Culture characteristics — Colonies on MEA reaching 36 mm diam, after 14 d at 15°C and 19 mm at 25°C in the dark, on OA reaching 40 mm at 15°C and 31 mm at 25°C , and on PDA reaching 35 mm at 15°C and attaining 18 mm at 25°C , respectively. Colonies on MEA with a distinct margin, flat, colony surface creamy to beige, reverse same colours. Colonies on OA with a smooth margin, flat, surface olive black, whitish at the margin, reverse same colours. Colonies on PDA with a distinct and regular margin, aerial mycelium sparse, grey-brown to light brown in the centre, buff to whitish at the margin, reverse same colours.

Additional specimens examined: **China:** Sichuan Province, Dagu Glacier, $\text{N}32^\circ13'14'' \text{E}102^\circ45'29''$, 4850 m, from soil, 1 May 2017, M-M Wang, culture DG975 = CGMCC3.20232; $\text{N}32^\circ8'19'' \text{E}102^\circ56'13''$, 2380 m, from soil, 1 May 2017, M-M Wang, culture DG1048 = CGMCC3.20191; DG1073 = CGMCC3.20235; DG1087 = CGMCC3.20236; DG1105 = CGMCC3.20197; Sichuan Province, Hailuoguo Glacier, $\text{N}29^\circ34'8'' \text{E}101^\circ59'36''$, 3180 m, from soil, 28 Apr. 2017, M-M Wang, culture HL876 = CGMCC3.20437; Yunnan Province, Baima Snow Mountain, $\text{N}29^\circ23'1'' \text{E}99^\circ0'20''$, 4366.2 m, from soil, 10 May 2017, M-M Wang, culture BM327 = CGMCC3.20181; BM360 = CGMCC3.20183; BM523 = CGMCC3.20230; BM816 = CGMCC3.20436; $\text{N}28^\circ22'59'' \text{E}99^\circ0'31''$, 4343 m, from soil, 10 May 2017, M-M Wang, culture BM857 = CGMCC3.20433; Yunnan Province, Mingyong Glacier, $\text{N}28^\circ27'27'' \text{E}98^\circ45'49''$, 2976 m, from soil, 9 May 2017, M-M Wang, culture MY474 = CGMCC3.20185; $\text{N}28^\circ27'28'' \text{E}98^\circ45'43''$, 3067 m, from soil, 9 May 2017, M-M Wang, culture MY492 = CGMCC3.20847; MY527 = CGMCC3.20848; MY588 = CGMCC3.20849; MY589 = CGMCC3.20850; MY873 = CGMCC3.20231; Yunnan Province, Yulong Snow Mountain, $\text{N}27^\circ10'55'' \text{E}100^\circ19'87''$, 4531 m, from soil, 7 May 2017, M-M Wang, culture YL73 = CGMCC3.20228; $\text{N}27^\circ11'17'' \text{E}100^\circ22'43''$, 3362 m, from water, 7 May 2017, M-M Wang, culture YL305 = CGMCC3.20435; YL319 = CGMCC3.20229; YL357 = CGMCC3.20182; YL414 = CGMCC3.20194.

Notes — More than half of the isolates in this study were identified as *Cadophora qinghai-tibetana* and they were isolated from soil and water samples of Yulong Glacier, Mingyong Glacier, Baima Snow Mountain in Yunnan Province and Dagu Glacier in Sichuan Province.

Strains of YL73 (from Yulong Snow Mountain), DG1048, DG1073, DG1087, DG1105 and DG1156 (from Dagu Glacier), MY527, MY588, MY589 and MY873 (from Mingyong Glacier) showed psychrophilic characteristics that they had optimum growth temperature at 15°C while the others had optimum growth temperature at 25°C. *C. qinghai-tibetana* had typical phialidic conidiogenesis and produced cylindrical to elongate-ellipsoidal conidia that were common in many *Cadophora* species, but all strains of this species formed a well-supported clade which was distinct from others in the multigene phylogenetic tree (Fig. 4).

Cadophora yulongensis Q-M Wang, B-Q Zhang & M-M Wang, **sp. nov.**

MycoBank No.: MB837894.

Figure 13

Etymology

Referring to Yulong Snow Mountain, the geographic origin of this species.

Type: **China:** Yunnan Provinces, Yulong Snow Mountain, N27°10'52" E100°19'84", 4531 m, from soil, 7 May 2017, M-M Wang, holotype HBU20010, culture ex-type YL814 = CGMCC3.20187.

Mycelium hyaline, septate, smooth-walled, branched, 1–3 µm wide. Conidiophores hyaline, smooth, often reduced to conidiogenous cells. Conidiogenous cells phialidic, located laterally or terminally, cylindrical or navicular, apex wedge, base truncate, hyaline, smooth-walled, straight or bent, 11.43–25.52 × 1.61–3.10 µm, collarettes evident, 2.10–4.54 µm long, opening 1.59–2.45 µm wide. Conidia hyaline, aseptate, smooth-walled, cylindrical, sporulation abundant, single, straight, 4.48–6.91 × 1.36–2.51 µm (mean = 5.50 ± 0.63 × 1.89 ± 0.29 µm, n = 30), L/W ratio = 2.91.

Culture characteristics — Colonies on MEA reaching 36 mm diam, after 14 d at 25°C in the dark, on OA and PDA reaching 38 mm and 28 mm diam, respectively. Colonies on MEA pale pink to whitish, white at the margin, reverse same colours. Colonies on OA black-gray with a grey-white margin, reverse same colours. Colonies on PDA grey to brown, margin wheat, cottony, reverse olive-brown to yellowish from centre to margin.

Notes — At the beginning, *Cadophora yulongensis* failed to produce conidia on MEA, OA and PDA medium. Other efforts including Pine needle medium culturing and H₂O₂ treatment (Xu et al, 2009) were also failed to induce sporulation until using slide culture technique. In the multigene phylogenetic tree (Fig. 4), *C. yulongensis* was closely related to lineages formed by species with holoblastic conidiogenesis, but this species was characterised by long cylindrical phialides and high conidium length/width ratio (2.91).

Discussion

The *Cadophora* species are reported worldwide, mainly as plant pathogens or root colonizers from northern temperate regions or decomposers from the cold Arctic and Antarctic environments. Because of the unique geographic location, the Qinghai-Tibet Plateau, which is also called 'the third pole', is more sensitive to changes of climate and surface conditions. Warm, moist air from the Indian Ocean flows up the valleys and is then blocked by huge mountains, leading to abundant rainfall in the southeast range of the plateau. Large numbers of marine glaciers form in this area. During the investigation of cold-adapted fungi from marine glaciers in the Qinghai-Tibet Plateau in 2017, 1208 fungal strains were isolated and identified based on preliminary analyses of generated ITS sequences. 41 isolates belonging to *Cadophora*, one of the most commonly encountered genera (*Cadophora*, *Geomyces* and *Pseudogymnoascus*, the other two will be discussed in another paper) were studied in detail. Our results showed that seven *Cadophora* species represented by 38 isolates were new to science and three isolates were identified as the known species of *C. malorum* and *C. novi-eboraci*. Temperature selective experiments also showed that many isolates had psychrophilic characteristics.

Because of limited discriminating morphological characteristics existed among *Cadophora* and the related genera, the genus has suffered taxonomic flux since the beginning of its establishment. DNA sequences have provided critical information for species delimitation and some *Cadophora* species with multiform morphological characters deviated from the original generic concept were often described based on molecular data. Day et al. (2012) tried to find some consistencies between morphological characteristics and phylogenetic relationships in *Cadophora* and the related genera. They hypothesized that the ancestral state for these taxa was the production of sclerotium-like heads of multiple phialides and clades derived from phialide arrangements agreed with those generated from rDNA ITS sequence analyses. Although ITS was useful for most fungal species identification, it often failed to discriminate species or even resulted in misleading informations in this group. E.g. according to the ITS analyses, *Cadophora malorum* CBS 165.42 nested within the *Cadophora*

luteo-olivacea clade, but in the TEF tree, *C. malorum* CBS 165.42 was strongly supported as the sister group to *C. luteo-olivacea* (Travadon et al. 2015) and the RPB1 gene can also resolve species relationships between *C. meredithiae* and *C. interclivum* better than the ITS (Wash et al. 2018); *C. microspora* with only teleomorph found was first identified based on ITS and morphological characteristics, but in recent studies, it was transferred to *Rhexocercosporidium* based on LSU and ITS analyses (Hyde et al. 2020). With more genes and species included, Maciá-Vicente et al. (2020) provided a more comprehensive overview about the ecology, morphology and phylogeny of *Cadophora*. Their results showed that the genus was apparently paraphyletic and encompassed a broad spectrum of morphologies and lifestyles. They tended to split the genus into three genera: one included those referred to as '*Cadophora* s. str. species' that evolved from an ancestor with phialidic conidiogenesis; the second included species like *C. interclivum*, *C. meredithiae*, *C. luteo-olivacea*, *C. malorum*, and *C. helianthi* that produced conidia phialidically but clustered in a separate clade; the third genus should take the name of *Collembolispora* and included *Cadophora* species with holoblastic conidiogenesis. But this drastic restructuring still need to be confirmed. Our multi-gene phylogenetic analyses also showed that *Cadophora* was paraphyletic and all the species involved clustered into two main clades (Fig. 4). Clade 1 comprised 18 *Cadophora* species (including five newly described in this study and the type of the genus) and three species belonging to other genera (*Cephalosporium gramineum*, *Mollisia cinerella* and *Phialophora dancoi*). This clade was similar to the '*Cadophora* s. str.' clade defined by Maciá-Vicente et al. (2020), just with more species involved. Although all species in Clade 1 had phialidic conidiogenesis, it is a bit arbitrary to combine *P. dancoi*, *M. cinerella* and *C. gramineum* into *Cadophora* at present, as we just assembled the ITS data sets of these three species to maximize taxon coverage and more exact morphological examinations also need to be done for these ex-types. Clade 2 included most members of Ploettnerulaceae and the rest *Cadophora* species. *C. constrictospora*, *C. gregata*, *C. helianthi*, *C. interclivum*, *C. luteo-olivacea*, *C. malorum*, *C. meredithiae* and *C. sabaouae* which had phialidic conidiogenesis clustered with those including *C. obovata*, *C. fallopiae*, *C. inflata* and two species of *Mastigosporium* which produced conidia with other kinds of conidogenesis; *C. gamsii*, *C. echinata*, *C. orchidicola*, *C. variabilis* and *C. yulongensis* formed a subclade with *Collembolispora barbata* and *Collembolispora aristate* and all of these species produce conidia through different ways; *C. antarctica*, *C. lacrimiformis* and *C. fascicularis* formed more distinct lineages. Thus, the currently circumscribed genus should be split into minor genera and the phylogenetic structure requires being clarified, but the introduction of more satisfying generic concepts depends on more news taxa involved.

Although *Cadophora* species were often encountered in cold environments, especially in the polar regions, most of them were psychrotolerant and had optimum growth temperature (OGT) near or above 20°C. The only psychrophilic species reported was *C. antarctica* which was isolated from a soil sample in King George Island (Antarctica) and had OGT at 15°C (Pedro et al. 2017). Travadon et al. (2015) hypothesized that the geographic distribution patterns of *Cadophora* species might reflect their adaptation to the contrasting environments: species recovered from cool areas normally had lower OGTs and those isolated from warmer regions tended to grow well at higher temperatures. This might be true in some cases and we also isolated many psychrophilic strains of this genus. Strains isolated from samples of Dagu Glacier (DG5, DG21, DG1048, DG1073, DG1087, DG1105 and DG1156), Mingyong Glacier (MY527, MY588, MY589, MY873 and Yulong glacier (YL73) all had optimum growth at 15°C, while others isolated from the same glaciers had OGTs of 25°C. Besides, strains isolated from the same sampling point and being identified as the same species (*C. qinghai-tibetana*) might have different OGTs. Environmental adaptations of fungal strains might be affected by many factors, such as temperature, humidity, radiation and substrates and they have to evolve complex abilities to survive in adverse environments. Therefore, it is necessary to test more physiological, biochemical characteristics or perform genome analyses to illustrate adaptation mechanisms of this important fungal group.

In this study, we proposed seven new species of *Cadophora* and some of them showed psychrophilic characteristics. With more species involved, the genus has become apparently paraphyletic and requires phylogenetic reconstruction. Thus, more comprehensive sampling is necessary for the creation of new generic concepts which could accommodate species deviated morphologically and phylogenetically in this important fungal group.

Declarations

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Authors' contributions

Sampling, molecular biology analysis: Manman Wang; fungal isolation: Manman Wang and Bingqian Zhang; description and phylogenetic analysis: Manman Wang, Qi-Ming Wang and Bingqian Zhang; microscopy: Manman Wang and Bingqian Zhang; writing—original draft

preparation: Manman Wang and Bingqian Zhang; writing—review and editing, Bingqian Zhang, Xiaoguang Li, Guojie Li, Qi-Ming Wang, Manman Wang. All authors read and approved the final manuscript.

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Availability of data and materials

All sequence data generated for this study (Table 2) can be accessed via GenBank: <https://www.ncbi.nlm.nih.gov/genbank/>. Alignments are available at TreeBase (<http://www.treebase.org>).

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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Figures

Figure 1

Sampling positions. a. Dagu Glacier; b. Yanzigou Glacier; c. Hailuoguo Glacier; d. Mingyong Glacier; e. Baima Snow Mountain; f. Yulong Snow Mountain.

Figure 2

The natural environment of the sampling sites. a. Meri Snow Mountain; b. Dagu Glacier; c–d. Baima Snow Mountain; e. Mingyong Glacier; f–g. Hailuoguo Glacier; h–l. Details of collecting samples in the glaciers and snow mountains.

Figure 3

Phylogenetic tree derived from Maximum Likelihood analysis based on LSU rDNA sequences. *Xylaria hypoxylon* CBS 120.16 was used as outgroup. Sequences generated from this study are printed in **bold** type. BP and PP values $\geq 70\%$ are shown at nodes. Thickened branches indicate strong support with ML/MP bootstrap values = BI posterior probabilities = 100%. Ex-type cultures are marked with a superscript T. The families the isolates belong to are highlighted by colored clades, and family names are listed to the right.

Figure 4

Phylogenetic tree derived from Maximum Likelihood analysis based on ITS, LSU, BT and TEF1- α combined sequence data. *Hyaloscypha finlandica* CBS 444.86^T and *Articulospora tetracladia* DSM 104345 were used as outgroup. Sequences generated from this study are printed in **bold** type. BP and PP values $\geq 70\%$ are shown at nodes. Thickened branches indicate strong support with ML/MP bootstrap values = BI posterior probabilities = 100%. Ex-type cultures are marked with a superscript T.

Figure 5

Cadophora caespitosa (CGMCC3.20179 – ex-type culture). **a–c** Front and reverse views of cultures on MEA, OA and PDA after 14 d (from left to right). **d** single phialide and conidia. **e–f** conidiophore and conidiogenous cells. **g** fascicle of phialides. **h** conidia. Scale bars = 10 μm

Figure 6

Cadophora indistincta (CGMCC3.20189 – ex-type culture). **a–c** Front and reverse views of cultures on MEA, OA and PDA after 14 d (from left to right). **d–f** single phialide and conidia. **g–i** conidiogenous cells. Scale bars = 10 μm

Figure 7

Cadophora inflata (CGMCC3.20186 – ex-type culture). **a–c** Front and reverse views of cultures on MEA, OA and PDA after 14 d (from left to right). **d** hyphal swellings. **e–f** microsclerotia-like bodies formed by mycelium. **g–k** conidia. Scale bars = 10 μ m

Figure 8

Cadophora magna (CGMCC3.20188 – ex-type culture). **a–c** Front and reverse views of cultures on MEA, OA and PDA after 14 d (from left to right). **d** single phialide producing conidium. **e–f** conidiophore and conidiogenous cells. **g** hyphae. **h** conidia. Scale bars = 10 μ m

Figure 9

Cadophora malorum (CGMCC3.20184 – isolate YL412). **a–c** Front and reverse views of cultures on MEA, OA and PDA after 14 d (from left to right). **d–e** fascicle of phialides. **f–j** conidiophore and conidiogenous cells. **k** conidia. Scale bars = 10 μm

Figure 10

Cadophora novi-eboraci (CGMCC3.20190 – isolate YZ1034). **a–c** Front and reverse views of cultures on MEA, OA and PDA after 14 d (from left to right); **d**. single phialide producing conidium. **e–f** conidiogenous cells and conidia. **g** hyphal swellings. **h** single phialide and conidia. **i** conidia. Scale bars = 10 μ m

Figure 11

Cadophora psychrophila (CGMCC3.20846 – ex-type culture). **a–c** Front and reverse views of cultures on MEA, OA and PDA after 14 d (from left to right). **d** some segments of swelled hypha. **e–i** conidiogenous cells and conidia. Scale bars = 10 μ m

Figure 12

Cadophora qinghai-tibetana (CGMCC3.20193 – ex-type culture). **a–c** Front and reverse views of cultures on MEA, OA and PDA after 14 d (from left to right). **d–f** conidiogenous cells and conidia. **g–h** phialide formed on hyphal coil. **i** hyphal coil. **j** conidia. Scale bars = 10 μm

Figure 13

Cadophora yulongensis (CGMCC3.20187 – ex-type culture). **a–c** Front and reverse views of cultures on MEA, OA and PDA after 14 d (from left to right). **d–g** conidiogenous cells and conidia. Scale bars = 10 μm