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Fusarium incarnatum-equiseti complex from China

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Key words

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new taxa
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taxonomy

Abstract The *Fusarium incarnatum-equiseti* species complex (FIESC) is shown to encompass 33 phylogenetic species, across a wide range of habitats/hosts around the world. Here, 77 pathogenic and endophytic FIESC strains collected from China were studied to investigate the phylogenetic relationships within FIESC, based on a polyphasic approach combining morphological characters, multi-locus phylogeny and distribution patterns. The importance of standardised cultural methods to the identification and classification of taxa in the FIESC is highlighted. Morphological features of macroconidia, including the shape, size and septum number, were considered as diagnostic characters within the FIESC. A multi-locus dataset encompassing the 5.8S nuclear ribosomal gene with the two flanking internal transcribed spacers (ITS), translation elongation factor (*EF-1α*), calmodulin (*CAM*), partial RNA polymerase largest subunit (*RPB1*) and partial RNA polymerase second largest subunit (*RPB2*), was generated to distinguish species within the FIESC. Nine novel species were identified and described. The *RPB2* locus is demonstrated to be a primary barcode with high success rate in amplification, and to have the best species delimitation compared to the other four tested loci.

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INTRODUCTION

The genus *Fusarium* is represented by 17 species complexes on the basis of multi-locus phylogenetic analyses (Laurence et al. 2011, Aoki et al. 2013, O'Donnell et al. 2013, Zhou et al. 2016, Sandoval-Denis et al. 2018a). The *Fusarium incarnatum-equiseti* species complex (FIESC) includes only a few formally described species characterised by the typically dorsiventral curvature of macroconidia and abundant chlamydospores, which range from being single or in chains or clumps, except for *F. scirpi* which lacks microconidia (Booth 1971, Leslie & Summerell 2006). However, confusion about species recognition of other isolates in this complex still exists due to significant genetic variability (Leslie & Summerell 2006). Members of the FIESC group are ubiquitous, mainly saprobes, pathogens or secondary invaders of environmental habitats, plants, humans and animals (Desjardins 2006, O'Donnell et al. 2009, 2012, Sandoval-Denis et al. 2018a). Furthermore, some of them pose threats to public health that can cause superficial infections such as keratitis on skin and nails, and deeply invasive and hematogenously disseminated infections with high mortality (e.g., FIESC phylogenetic species 15, 25; O'Donnell et al. 2009, 2012) and some produce mycotoxins (e.g., trichothecenes) on cereals (e.g., FIESC phylogenetic species 5, 31; Villani et al. 2016).

Phylogenetic analyses of *RPB1-RPB2* indicated that the FIESC represented a monophyletic lineage in the *Gibberella* clade, closely related to the *F. chlamydosporum* and *F. sambucinum* species complexes (Ma et al. 2013, O'Donnell et al. 2013). These three species complexes clustered as a terminal group in the *Gibberella* clade, which is distant from other major groups encompassing the *F. fujikuroi*, *F. nisikadoi* and *F. oxysporum* species complexes and other species (Ma et al. 2013, O'Donnell et al. 2013). Some species in these groups produce a *Gibberella* sexual morph such as *F. fujikuroi* (O'Donnell et al. 1998a), or may have a cryptic sexual morph as revealed by the analysis of mating type genes such as in *F. oxysporum* (Arie et al. 2000, Ma et al. 2013, Woloshuk & Shim 2013).

Species delimitation and taxonomy within the FIESC is still unclear. Due to morphological homoplasy and high similarity in ITS sequence (98–100 %), members of this group were usually identified as either *F. equiseti* or *F. incarnatum* in previous studies (Khoa et al. 2004, Leslie & Summerell 2006, Marín et al. 2012). The results of multi-locus phylogenetic analyses and Genealogical Concordance Phylogenetic Species Recognition (GCPSR) revealed that the FIESC includes 32 phylogenetic species which are separated in two major clades, the *Equiseti* clade (16 phylogenetic species) and the *Incarnatum* clade (16 phylogenetic species), but most of them remain unnamed (O'Donnell et al. 2009, 2012, Villani et al. 2016). So far, only six species have been introduced, viz. *F. compactum*, *F. equiseti*, *F. incarnatum*, *F. lacertarum*, *F. scirpi* and *F. sulawense* (Saccardo 1886, Raillo 1950, Subrahmanyam 1983, Burgess et al. 1985, Maryani et al. 2019b). However, these six species have not always been accepted by mycologists. For instance, *F. scirpi* was considered as a synonym of *F. equiseti* by Gordon (1952) and Booth (1971), but recognised as a distinct species from *F. equiseti* by Gerlach & Nirenberg (1982) and Nelson et al. (1983). *Fusarium scirpi* is currently listed as a synonym of *F. acuminatum* in the Index Fungorum (http://www.indexfungorum.org/), but as a separate species in MycoBank (http://www.mycobank.org/).

Previous studies based on molecular data revealed a high phylogenetic diversity of the FIESC strains from plant sources, and a total of 18 phylogenetic species associated with plants were reported worldwide (O'Donnell et al. 2009, 2012), among which seven species have been recorded on wheat in Spain (Castellá & Cabañes 2014), 15 on maize and banana fruit in China (Munaut et al. 2013) and 12 on cereals in Europe and North America (Villani et al. 2016). The investigation of

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Table 1 Strains examined in this study, with information about host/habitat, location and GenBank accessions of sequences.

Species	Phylogenetic species	Strain number and status*	Isolate habitat/host	Location	ITS	*EF-1α*	*CAM*	*RPB1*	*RPB2*
F. arcuatisporum	FIESC 7	LC11639	*Oryza* sp.	Hainan, China	MK280840	MK289586	MK289658	MK289798	MK289736
		LC6026	*Nelumbo nucifera* leaf	Jiangxi, China	MK280792	MK289585	MK289667	MK289800	MK289770
		LC12147 = CGMCC3.19493 (T)	*Brassica campestris* pollen	Hubei, China	MK280802	MK289584	MK289697	MK289799	MK289739
		NRRL 32997 = UTHSC 99-423	Human toenail	Colorado, America	GQ505713	GQ505624	GQ505536	HM347164	GQ505802
F. citri	FIESC 29	LC4879	*Amygdalus triloba*	Beijing, China	MK280820	MK289615	MK289665	MK289827	MK289768
		LC6896 = CGMCC3.19467 (T)	*Citrus reticulata* leaf	Hunan, China	MK280803	MK289617	MK289668	MK289828	MK289771
		LC7922	*Capsicum* sp.	Shandong, China	MK280817	MK289634	MK289687	MK289829	MK289788
		LC7937	*Capsicum* sp.	Shandong, China	MK280797	MK289640	MK289693	MK289830	MK289794
		NRRL 25084 = ARSEF 1641	*Adelphocoris* sp.	Austria	JF740883	JF740715	–	–	–
		NRRL 52765 = ARSEF 2304	*Heteropsylla cubana*	Papua New Guinea	–	JF740839	–	–	JF741165
F. compactum	FIESC 3	NRRL 28029 = CDC B-3335	Human eye	California, America	GQ505691	GQ505602	GQ505514	HM347150	GQ505780
		NRRL 36318 = CBS 185.31	Unknown	Unknown	GQ505735	GQ505646	GQ505558	–	GQ505824
		NRRL 36323 = CBS 186.31 (T)	*Gossypium* sp.	England	GQ505737	GQ505648	GQ505560	–	GQ505826
F. equiseti	FIESC 14	NRRL 20697 = CBS 245.61	Beet	Chile	GQ505683	GQ505594	GQ505506	JX171481	GQ505772
		NRRL 26419 = CBS 307.94, BBA 68556 (NT)	Soil	Germany	GQ505688	GQ505599	GQ505511	–	GQ505777
		NRRL 36136 = CBS 107.07, IMI 091982	Unknown	Unknown	GQ505733	GQ505644	GQ505556	–	GQ505822
		NRRL 36321 = CBS 185.34	Soil	Netherlands	GQ505736	GQ505647	GQ505559	–	GQ505825
		NRRL 36466 = CBS 414.86	*Solanum tuberosum*	Denmark	GQ505742	GQ505653	GQ505565	–	GQ505831
		NRRL 43636 = UTHSC 06-170	Dog	Texas, America	GQ505752	GQ505663	GQ505574	HM347189	GQ505841
F. guilinense	FIESC 21	LC12160 = CGMCC3.19495 (T)	*Musa nana* leaf	Guangxi, China	MK280837	MK289594	MK289652	MK289831	MK289747
		NRRL 13335 = FRC R-2138	Alfalfa	Australia	GQ505679	GQ505590	GQ505502	–	GQ505768
		NRRL 32865 = FRC R-8480	Human endocarditis	Brazil	GQ505703	GQ505614	GQ505526	HM347161	GQ505792
F. hainanense	FIESC 26	LC11638 = CGMCC3.19478 (T)	*Oryza* sp. stem	Hainan, China	MK280836	MK289581	MK289657	MK289833	MK289735
		LC12161	*Musa nana* leaf	Guangxi, China	MK280793	MK289595	MK289648	MK289832	MK289748
		NRRL 26417 = CBS 544.96	Leaf litter	Cuba	GQ505687	GQ505598	GQ505510	JX171522	GQ505776
		NRRL 28714 = ATCC 74289	*Acacia* sp. branch	Costa Rica	GQ505693	GQ505604	GQ505516	–	GQ505782
F. humuli	FIESC 33	CQ1027	*Ligustrun lucidum* leaf	Jiangsu, China	MK280843	MK289567	MK289709	MK289838	MK289721
		CQ1032	*Cedrela* sp. leaf	Jiangsu, China	MK280844	MK289568	MK289710	MK289839	MK289722
		CQ1039 = CGMCC3.19374 (T)	*Humulus scandens* leaf	Jiangsu, China	MK280845	MK289570	MK289712	MK289840	MK289724
		CQ1048	*Viburnum* sp. leaf	Jiangsu, China	MK280850	MK289571	MK289713	MK289841	MK289725
		CQ1073	*Liquidambar formosana* leaf	Jiangsu, China	MK280848	MK289572	MK289714	MK289842	MK289726
		CQ1133	*Vinca major* leaf	Jiangsu, China	MK280847	MK289575	MK289717	MK289843	MK289729
		CQ969	*Rosa sempervirens* leaf	Jiangsu, China	MK280851	MK289576	MK289718	MK289844	MK289730
		CQ970	*Rosa sempervirens* leaf	Jiangsu, China	MK280849	MK289577	MK289719	MK289845	MK289731
		CQ975	*Paederia foetida* leaf	Jiangsu, China	MK280846	MK289578	MK289720	MK289846	MK289732
		LC12158	*Musa nana* leaf	Guangdong, China	MK280823	MK289592	MK289645	MK289834	MK289745
		LC12159	*Musa nana* leaf	Guangdong, China	MK280827	MK289593	MK289646	MK289835	MK289746
		LC4490	*Osmanthus* sp.	Jiangxi, China	MK280826	MK289614	MK289664	MK289836	MK289767
		LC7003	*Musa paradisiaca*	Hainan, China	MK280833	MK289623	MK289674	MK289837	MK289777
F. ipomoeae	FIESC 1	CQ1099	*Rhododendron pulchrum* leaf	Jiangsu, China	MK280853	MK289573	MK289715	MK289861	MK289727
		CQ1132	*Vinca major* leaf	Jiangsu, China	MK280854	MK289574	MK289716	MK289862	MK289728
		LC0166	*Solanum lycopersicum* fruit	Beijing, China	MK280780	MK289579	MK289659	MK289848	MK289733
		LC0455	*Hosta* sp.	Beijing, China	MK280819	MK289580	MK289660	MK289849	MK289734
		LC12162	*Musa nana* leaf	Guangxi, China	MK280795	MK289596	MK289655	MK289847	MK289749
		LC12163	*Hibiscus syriacus*	Fujian, China	MK280790	MK289597	MK289700	MK289857	MK289750
		LC12164	*Hibiscus syriacus*	Fujian, China	MK280822	MK289598	MK289701	MK289858	MK289751
		LC12165 = CGMCC3.19496 (T)	*Ipomoea aquatica* leaf	Fujian, China	MK280832	MK289599	MK289704	MK289859	MK289752
		LC12166	*Lagenaria siceraria*	Fujian, China	MK280791	MK289600	MK289706	MK289860	MK289753
		LC5912	Submerged wood	Jiangxi, China	MK280821	MK289616	MK289666	MK289850	MK289769
		LC6926	*Oryza sativa*	Hubei, China	MK280799	MK289619	MK289670	MK289851	MK289773

Table 1 (cont.)

Species	Phylogenetic species	Strain number and status*	Isolate habitat/host	Location	ITS	*EF-1α*	*CAM*	*RPB1*	*RPB2*
F. ipomoeae (cont.)		LC7150	Bamboo	Jiangxi, China	MK280818	MK289627	MK289678	MK289852	MK289781
		LC7923	*Capsicum* sp.	Shandong, China	MK280800	MK289635	MK289688	MK289853	MK289789
		LC7925	*Capsicum* sp.	Shandong, China	MK280796	MK289636	MK289689	MK289854	MK289790
		LC7936	*Capsicum* sp.	Shandong, China	MK280785	MK289639	MK289692	MK289855	MK289793
		LC7940	*Capsicum* sp.	Shandong, China	MK280798	MK289642	MK289695	MK289856	MK289796
		NRRL 34034 = UTHSC 94-1167	Human leg	Arizona, America	GQ505725	GQ505636	GQ505548	–	GQ505814
		NRRL 34039 = UTHSC 96-1394	Human	Connecticut, America	GQ505728	GQ505639	GQ505551	–	GQ505817
		NRRL 43637 = UTHSC 05-1729	Dog	Pennsylvania, America	GQ505753	GQ505664	GQ505575	–	GQ505842
		NRRL 43640 = UTHSC 04-123	Dog nose	Texas, America	GQ505756	GQ505667	GQ505578	HM347191	GQ505845
		NRRL 45996 = UTHSC 03-3101	Human sinus	New York, America	GQ505760	GQ505671	GQ505582	–	GQ505849
F. irregulare	FIESC 15	LC12145 = WMM0324	Bamboo	Guangdong, China	MK280830	MK289582	MK289681	MK289864	MK289737
		LC12146 = WMM0325	Bamboo	Guangdong, China	MK280831	MK289583	MK289682	MK289865	MK289738
		LC7188 = CGMCC3.19489 (T)	Bamboo	Guangdong, China	MK280829	MK289629	MK289680	MK289863	MK289783
		NRRL 31160 = MDA 3	Human lung	Texas, America	GQ505696	GQ505607	GQ505519	–	GQ505785
		NRRL 32175 = MDA F10	Human sputum	Texas, America	GQ505698	GQ505609	GQ505521	–	GQ505787
		NRRL 32181 = MDA F20	Human blood	Oklahoma, America	GQ505699	GQ505610	GQ505522	–	GQ505788
		NRRL 32182 = MDA F22	Human blood	Texas, America	GQ505700	GQ505611	GQ505523	–	GQ505789
		NRRL 32869 = FRC R-9445	Human cancer patient	Texas, America	GQ505707	GQ505618	GQ505530	–	GQ505796
		NRRL 32994 = UTHSC 00-494	Human ethmoid sinus	Texas, America	GQ505710	GQ505621	GQ505533	–	GQ505799
		NRRL 32995 = UTHSC 99-1964	Human sinus	Texas, America	GQ505711	GQ505622	GQ505534	–	GQ505800
		NRRL 32996 = UTHSC 99-1741	Human leg wound	Texas, America	GQ505712	GQ505623	GQ505535	–	GQ505801
		NRRL 34001 = UTHSC 95-1945	Human foot wound	Texas, America	GQ505714	GQ505625	GQ505537	–	GQ505803
		NRRL 34006 = UTHSC 93-2692	Human eye	Texas, America	GQ505719	GQ505630	GQ505542	HM347169	GQ505808
		NRRL 34007 = UTHSC 93-933	Human sputum	Texas, America	GQ505720	GQ505631	GQ505543	–	GQ505809
		NRRL 34008 = UTHSC 92-1955	Human lung	Texas, America	GQ505721	GQ505632	GQ505544	–	GQ505810
		NRRL 34010 = UTHSC 02-1698	Human maxillary sinus	Texas, America	GQ505722	GQ505633	GQ505545	–	GQ505811
		NRRL 43619 = UTHSC 05-2847	Human finger	Texas, America	GQ505748	GQ505659	GQ505570	–	GQ505837
F. lacertarum	FIESC 4	LC7927	*Capsicum* sp.	Shandong, China	MK280838	MK289637	MK289690	MK289866	MK289791
		LC7931	*Capsicum* sp.	Shandong, China	MK280801	MK289638	MK289691	MK289867	MK289792
		LC7942	*Capsicum* sp.	Shandong, China	MK280834	MK289643	MK289696	MK289868	MK289797
		NRRL 20423 = IMI 300797 (T)	Lizard skin	India	GQ505682	GQ505593	GQ505505	JX171467	GQ505771
		NRRL 36123 = CBS 102300, BBA 70843	Unknown	Unknown	GQ505732	GQ505643	GQ505555	–	GQ505821
F. luffae	FIESC 18	CQ1038	*Humulus scandens* leaf	Jiangsu, China	MK280852	MK289569	MK289711	MK289870	MK289723
		LC12167 = CGMCC3.19497 (T)	*Luffa aegyptiaca*	Fujian, China	MK280807	MK289601	MK289698	MK289869	MK289754
		NRRL 32522 = Loyola W-14182	Human diabetic cellulitis	Illinois, America	GQ505701	GQ505612	GQ505524	HM347158	GQ505790
		NRRL 31167	Human sputum	Texas, America	GQ505697	GQ505608	GQ505520	–	GQ505786
F. nanum	FIESC 25	LC12168 = CGMCC3.19498 (T)	*Musa nana* leaf	Guangxi, China	MK280794	MK289602	MK289651	MK289871	MK289755
		LC1384	*Solanum lycopersicum*	Saudi Arabia	MK280842	MK289611	MK289661	MK289872	MK289764
		LC1385	*Solanum lycopersicum*	Saudi Arabia	MK280781	MK289612	MK289662	MK289873	MK289765
		LC1516	*Solanum lycopersicum*	Saudi Arabia	MK280782	MK289613	MK289663	MK289874	MK289766
		NRRL 22244 = H.-K. Chen F64	*Oryza* sp.	China	GQ505685	GQ505596	GQ505508	–	GQ505774
		NRRL 32868 = FRC R-8880	Human blood	Texas, America	GQ505706	GQ505617	GQ505529	HM347163	GQ505795
		NRRL 32993 = UTHSC 00-755	Human nasal tissue	Texas, America	GQ505709	GQ505620	GQ505532	–	GQ505798
F. scirpi	FIESC 9	NRRL 13402 = FRC R-6363	Pine soil	Australia	GQ505681	GQ505592	GQ505504	–	GQ505770
		NRRL 26992 = CBS 610.95	Soil	France					
		NRRL 29134 = CBS 448.84	Pasture soil	Australia	GQ505694	GQ505605	GQ505517	–	GQ505783
		NRRL 36478 = CBS 447.84	Pasture soil	Australia	GQ505743	GQ505654	GQ505566	–	GQ505832
F. sulawense	FIESC 16 & 17	LC12148	*Musa nana* leaf	Guangdong, China	MK280778	MK289587	MK289644	MK289801	MK289740
		LC12149	*Musa nana* leaf	Guangdong, China	MK280783	MK289588	MK289647	MK289802	MK289741
		LC12151	*Musa nana* fruit	Guangxi, China	MK280825	MK289589	MK289649	MK289803	MK289742
		LC12152	*Musa nana* fruit	Guangxi, China	MK280824	MK289590	MK289650	MK289804	MK289743

Table 1 (cont.)

Species	Phylogenetic species	Strain number and status*	Isolate habitat/host	Location	ITS	*EF-1α*	*CAM*	*RPB1*	*RPB2*
F. sulawense (cont.)		LC12153	*Musa nana* leaf	Guangxi, China	MK280779	MK289591	MK289654	MK289806	MK289744
		LC12169	*Musa nana* stem	Guangxi, China	MK280784	MK289603	MK289653	MK289805	MK289756
		LC12170	*Musa nana* leaf	Guangxi, China	MK280841	MK289604	MK289656	MK289807	MK289757
		LC12173	*Luffa aegyptiaca*	Fujian, China	MK280788	MK289605	MK289699	MK289821	MK289758
		LC12174	*Ipomoea batatas*	Fujian, China	MK280815	MK289606	MK289702	MK289822	MK289759
		LC12175	*Ipomoea aquatica*	Fujian, China	MK280808	MK289607	MK289703	MK289823	MK289760
		LC12176	*Luffa aegyptiaca*	Fujian, China	MK280839	MK289608	MK289705	MK289824	MK289761
		LC12177	*Colocasia esculenta*	Fujian, China	MK280809	MK289609	MK289707	MK289825	MK289762
		LC12178	*Syngonium auritum*	Guangdong, China	MK280789	MK289610	MK289708	MK289826	MK289763
		LC6897	*Citrus reticulata*	Hunan, China	MK280810	MK289618	MK289669	MK289808	MK289772
		LC6928	*Oryza sativa*	Hubei, China	MK280835	MK289620	MK289671	MK289809	MK289774
		LC6936	*Oryza sativa*	Hubei, China	MK280828	MK289621	MK289672	MK289810	MK289775
		LC6990	*Musa paradisiaca* leaf	Hainan, China	MK280814	MK289622	MK289673	MK289811	MK289776
		LC7014	*Musa paradisiaca* leaf	Hainan, China	MK280786	MK289624	MK289675	MK289812	MK289778
		LC7019	*Musa paradisiaca* leaf	Hainan, China	MK280816	MK289625	MK289676	MK289813	MK289779
		LC7040	*Musa paradisiaca* leaf	Hainan, China	MK280787	MK289626	MK289677	MK289814	MK289780
		LC7157	Bamboo leaf	Jiangxi, China	MK280804	MK289628	MK289679	MK289815	MK289782
		LC7210	Bamboo leaf	Jiangxi, China	MK280812	MK289630	MK289683	MK289816	MK289784
		LC7842	*Zea* sp.	Hainan, China	MK280813	MK289631	MK289684	MK289817	MK289785
		LC7919	*Capsicum* sp. fruit	Shandong, China	MK280811	MK289632	MK289685	MK289818	MK289786
		LC7920	*Capsicum* sp. fruit	Shandong, China	MK280805	MK289633	MK289686	MK289819	MK289787
		LC7939	*Capsicum* sp. fruit	Shandong, China	MK280806	MK289641	MK289694	MK289820	MK289795
		NRRL 32864 = FRC R-7245	Human	Texas, America	GQ505702	GQ505613	GQ505525	HM347160	GQ505791
		NRRL 34004 = UTHSC 94-2581	Human	Texas, America	GQ505717	GQ505628	GQ505540	HM347167	GQ505806
		NRRL 34056 = Loyola M54234	Human bronchial wash	Illinois, America	GQ505729	GQ505640	GQ505552	–	GQ505818
		NRRL 34059 = Loyola S8158	Human blood	Illinois, America	GQ505730	GQ505641	GQ505553	–	GQ505819
		NRRL 34070 = Loyola W37591	Tortoise	Illinois, America	GQ505731	GQ505642	GQ505554	–	GQ505820
		NRRL 36548 = CBS 190.60	*Musa nana*	Congo	GQ505744	GQ505655	GQ505567	–	GQ505833
		NRRL 43730 = CDC 2006743605	Contact lens	Mississippi, America	EF453193	GQ505669	GQ505580	–	GQ505847
	FIESC 2	NRRL 36401 = CBS 264.50	*Gossypium* sp.	Mozambique	GQ505740	GQ505651	GQ505563	–	GQ505829
		NRRL 36448 = CBS 384.92	*Phaseolus vulgaris* seed	Sudan	GQ505741	GQ505652	GQ505564	–	GQ505830
	FIESC 5	NRRL 25795 = CBS 394.93, BBA 64265	*Disphyma crassifolium* seed	Germany	GQ505686	GQ505597	GQ505509	–	GQ505775
		NRRL 32871 = FRC R-9561	Human abscess	Texas, America	GQ505708	GQ505619	GQ505531	–	GQ505797
		NRRL 34032 = UTHSC 98-2172	Human abscess	Texas, America	GQ505724	GQ505635	GQ505547	HM347171	GQ505813
		NRRL 34035 = UTHSC 91-569	Human sinus	Colorado, America	GQ505726	GQ505637	GQ505549	–	GQ505815
		NRRL 34037 = UTHSC 02-966	Human abscess	Colorado, America	GQ505727	GQ505638	GQ505550	–	GQ505816
		NRRL 45995 = UTHSC 02-966	Human abscess	Colorado, America	GQ505759	GQ505670	GQ505581	–	GQ505848
		NRRL 45997 = UTHSC 04-1902	Human sinus	Colorado, America	GQ505761	GQ505672	GQ505583	–	GQ505850
	FIESC 6	NRRL 43638 = UTHSC R-3500	Manatee	Florida, America	GQ505754	GQ505665	GQ505576	–	GQ505843
		NRRL 43694 = CDC 2006743607	Human eye	Texas, America	GQ505757	GQ505668	GQ505579	HM347193	GQ505846
		NRRL 45998 = UTHSC 06-2315	Human toe	Texas, America	GQ505762	GQ505673	GQ505584	–	GQ505851
	FIESC 8	NRRL 43498	Human eye	Pennsylvania, America	GQ505747	GQ505658	–	HM347181	GQ505836
		NRRL 5537 = ATCC 28805	*Festuca* sp.	Missouri, America	GQ505677	GQ505588	GQ505500	–	GQ505766
	FIESC 10	NRRL 3020 = FRC R-6053, 7.12 MRC	Unknown	Unknown	GQ505675	GQ505586	GQ505498	–	GQ505764
		NRRL 3214 = FRC R-6054, 7.13 MRC	Unknown	Unknown	GQ505676	GQ505587	GQ505499	–	GQ505765
	FIESC 11	NRRL 36372 = CBS 235.79	Air	Antilles, Netherlands	GQ505738	GQ505649	GQ505561	–	GQ505827
	FIESC 12	NRRL 26921 = CBS 731.87	*Triticum* sp.	Germany	GQ505689	GQ505600	GQ505512	–	GQ505778
		NRRL 31011 = BBA 69079	*Thuja* sp.	Germany	GQ505695	GQ505606	GQ505518	–	GQ505784
		NRRL 36269 = CBS 162.57	*Pinus nigra* seedling	Croatia	GQ505734	GQ505645	GQ505557	–	GQ505823
		NRRL 36392 = CBS 259.54	Unknown plant seedling	Germany	GQ505739	GQ505650	GQ505562	–	GQ505828
		NRRL 6548 = IMI 112503	*Triticum* sp.	Germany	GQ505678	GQ505589	GQ505501	–	GQ505767
	FIESC 13	NRRL 43635 = UTHSC 06-638	Horse	Nebraska	GQ505751	GQ505662	GQ505573	HM347188	GQ505840
	FIESC 19	NRRL 43639 = UTHSC 04-135	Manatee	Florida, America	GQ505755	GQ505666	GQ505577	HM347190	GQ505844

Table 1 (cont.)

Species	Phylogenetic species	Strain number and status*	Isolate habitat/host	Location	ITS	*EF-1α*	*CAM*	*RPB1*	*RPB2*
	FIESC 20	NRRL 34003 = UTHSC 95-28	Human sputum	Texas, America	GQ505716	GQ505627	GQ505539	HM347166	GQ505805
		NRRL 36575 = CBS 976.97	*Juniperus chinensis* leaf	Hawaii, America	GQ505745	GQ505656	GQ505568	–	GQ505834
	FIESC 22	NRRL 34002 = UTHSC 95-1545	Human ethmoid sinus	Texas, America	GQ505715	GQ505626	GQ505538	HM347165	GQ505804
	FIESC 23	NRRL 13379 = FRC R-5198, BBA 62200	*Oryza sativa*	India	GQ505680	GQ505591	GQ505503	–	GQ505769
		NRRL 32866 = FRC R-8822	Human cancer patient	Texas, America	GQ505704	GQ505615	GQ505527	HM347162	GQ505793
		NRRL 32867 = FRC R-8837	Human	Texas, America	GQ505705	GQ505616	GQ505528	–	GQ505794
	FIESC 24	NRRL 34005 = UTHSC 94-2471	Human intravitreal fluid	Minnesota, America	GQ505718	GQ505629	GQ505541	HM347168	GQ505807
		NRRL 43297 = W. Elmer 22	*Spartina rhizomes*	Connecticut, America	GQ505746	GQ505657	GQ505569	–	GQ505835
	FIESC 27	NRRL 20722 = IMI 190455	*Chrysanthemum* sp.	Kenya	GQ505684	GQ505595	GQ505507	–	GQ505773
	FIESC 28	NRRL 28577 = CBS 430.81	Grave stone	Romania	GQ505692	GQ505603	GQ505515	–	GQ505781
	FIESC 30	NRRL 52758 = ARSEF 4714	*Prosapia* nr. *bicincta* on Cynodon	Costa Rica	JF740925	JF740833	–	–	JF741159
	FIESC 31	ITEM11401	*Avena sativa*	Canada	–	LN901578	LN901594	–	LN901611
		ITEM13601	*Zea* sp.	Netherlands	–	–	–	–	LN901614
	FIESC 32	CBS 143595	*Ganoderma* sp.	Iran	LT970814	LT970778	LT970731	–	LT970750
		CBS 143596	*Stereum rsutum*	Iran	LT970815	LT970779	LT970732	–	LT970751
		CBS 143597	Smut	Iran	LT970820	LT970784	LT970737	–	LT970756
		CBS 143598	Smut	Iran	LT970816	LT970780	LT970733	–	LT970752
		CBS 143600	Smut	Iran	LT970818	LT970782	LT970735	–	LT970754
		CBS 143603	Smut	Iran	LT970817	LT970781	LT970734	–	LT970753
		CBS 143606	Smut	Iran	LT970819	LT970783	LT970736	–	LT970755
F. polyphialidicum	–	NRRL 13459 = CBS 961.87 (T)	Plant debris	South Africa	GQ505763	GQ505674	GQ505585	–	GQ505852

* T = Ex-type, NT = Neotype.

plant-associated *Fusarium* in China could be dated back to Bugnicourt (1939), with *F. equiseti* isolated from three plants (i.e., *Bruguiera gymnorhiza*, *Phaseolus lunatus* and *Ricinus communis*). During the investigation of pathogenic and endophytic fusaria associated with plants, 77 strains were isolated from more than 22 plant species and identified as members of FIESC. By using morphological characters and multi-locus phylogenetic analyses, our aims were to:

i. clarify the phylogenetic and taxonomic relationships of species within the FIESC; and
ii. describe novel species within the FIESC.

MATERIAL AND METHODS

Isolation

Diseased and healthy plant tissues, including stems, leaves and pollen, were collected from eight provinces (Fujian, Guangdong, Guangxi, Hainan, Hubei, Hunan, Jiangxi and Shandong) and Beijing in China. Tissue pieces (4 mm^2) were taken from the margin of leaf or stem spots as well as healthy sections, consecutively immersed in 75 % ethanol for 1 min, 5 % NaClO for 3 min, 70 % ethanol for 1 min, and rinsed in sterile distilled water for 30 s. Tissue pieces were blotted dry in sterile paper towels and incubated on 1/4 strength potato dextrose agar (PDA) containing ampicillin and streptomycin (50 mg/L each) (Liu et al. 2015). Isolates were retrieved from pollen using the plate dilution method. One g pollen was suspended in 9 mL sterile water. The suspension was shaken on the Vortex vibration meter for 10 min. The extract was diluted to a series of concentrations, i.e., 10^{-2}, 10^{-3}, 10^{-4} and 10^{-5}. For each concentration, 200 µL suspension was spread onto 1/4 strength PDA with three replicates. All plates were incubated at room temperature and examined every 2 d. Individual colonies were picked up with a sterilized needle and transferred onto new PDA plates. All the cultures were then purified using an optimized protocol of single spore isolation (Zhang et al. 2013).

All seventy-seven isolates examined in this study were deposited in Lei Cai's personal culture collection (LC). Information of isolates including geographic distribution and host/habitat are listed in Table 1. Type specimens of new species were deposited in the Mycological Herbarium of the Institute of Microbiology, Chinese Academy of Sciences, Beijing, China (HAMS), and living ex-type cultures in the China General Microbiological Culture Collection Centre (CGMCC), with duplicates deposited in the culture collection (CBS) of the Westerdijk Fungal Biodiversity Institute, in Utrecht, the Netherlands.

Morphological studies

Examined isolates were incubated on synthetic nutrient poor agar (SNA; Nirenberg 1976) for 7 d at 25 °C. Approximately 5 × 5 mm agar pieces were cut from the edge of colonies and transferred onto media for morphological characterisation. Cultural characteristics, including colony morphology, pigmentation and odour, were observed after 7 d incubation in the dark on PDA, oatmeal agar (OA) and SNA (Nirenberg 1976). Colours were rated according to the colour charts of Kornerup & Wanscher (1978). Sporodochia were induced by incubating under a 12/12 h near-ultraviolet light/dark cycle, on SNA and water agar (WA) amended with sterilised pieces of carnation leaves (Snyder & Hansen 1947, Fisher et al. 1982) at 25 °C, respectively. Micromorphological characteristics were examined and photo-documented with water as mounting medium on a Nikon 80i microscope with Differential Interference Contrast (DIC) optics, and a Nikon SMZ1500 dissecting microscope. For each species, 30 conidiogenous cells, 50 macroconidia and 50 chlamydospores were mounted and randomly measured to calculate the mean size and standard deviation (SD).

Table 2 Primer pairs, PCR amplification procedures and references using in this study.

Locus	Primer		PCR amplification procedures	Reference
	Designation	Sequence (5'-3')*		
ITS	ITS5	GGAAGTAAAAGTCGTAACAAGG	94 °C 90 s; 35 cycles of 94 °C 45 s, 55 °C 45 s, 72 °C 1 min; 72 °C 10 min; 10 °C soak	White et al. (1990)
	ITS4	TCCTCCGCTTATTGATATGC		White et al. (1990)
EF-1α	EF1	ATGGGTAAGGARGACAAGAC	94 °C 90 s; 35 cycles of 94 °C 45 s, 55 °C 45 s, 72 °C 1 min; 72 °C 10 min; 10 °C soak	O'Donnell et al. (1998b)
	EF2	GGARGTACCAGTSATCATG		O'Donnell et al. (1998b)
CAM	CL1	GARTWCAAGGAGGCCTTCTC	94 °C 90 s; 35 cycles of 94 °C 45 s, 55 °C 45 s, 72 °C 1 min; 72 °C 10 min; 10 °C soak	O'Donnell et al. (2000)
	CL2A	TTTTTGCATCATGAGTTGGAC		O'Donnell et al. (2000)
RPB1	Fa	CAYAARGARTCYATGATGGGWC	94 °C 90 s; 5 cycles of 94 °C 45 s, 58 °C 45 s, 72 °C 2 min; 5 cycles of 94 °C 45 s, 57 °C 45 s, 72 °C 2 min; 35 cycles of 94 °C 45 s, 56 °C 45s, 72 °C 2 min; 72 °C 10 min; 10 °C soak	O'Donnell et al. (2010)
	G2R	GTCATYTGDGTDGCDGGYTCDCC		O'Donnell et al. (2010)
RPB2	5f2	GGGGWGAYCAGAAGAAGGC	94 °C 90 s; 5 cycles of 94 °C 45 s, 58 °C 45 s, 72 °C 2 min; 5 cycles of 94 °C 45 s, 57 °C 45 s, 72 °C 2 min; 35 cycles of 94 °C 45 s, 56 °C 45 s, 72 °C 2 min; 72 °C 10 min; 10 °C soak	Reeb et al. (2004)
	11ar	GCRTGGATCTTRTCRTCSACC		Liu et al. (1999)

* R = A or G; s = C or G; W = A or T; Y = C or T.

DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted from fungal mycelia grown on PDA, using a modified CTAB protocol as described in Guo et al. (2000). Five loci, including the 5.8S nuclear ribosomal RNA gene with the two flanking internal transcribed spacer (ITS), translation elongation factor (*EF-1α*), calmodulin (*CAM*), partial RNA polymerase largest subunit (*RPB1*) and partial RNA polymerase second largest subunit (*RPB2*) gene regions, were amplified and sequenced, respectively. The primer pairs and PCR amplification procedures following protocols described by Crous et al. (2009) are listed in Table 2. PCR amplifications were performed in a reaction mixture consisting of 12.5 µL 2 × Taq PCR Master Mix (Vazyme Biotech Co.,Ltd, Nanjing, China), 1 µL each of 10 µM primers, 1 µL of the undiluted genomic DNA, adjusted to a final volume of 25 µL with distilled deionized water. The PCR products were visualised on 1 % agarose electrophoresis gel. Sequencing was done bi-directionally, conducted by the TIANYI HUIYUAN Company (Beijing, China). Consensus sequences were obtained using SeqMan of the Lasergene software package v. 14.1 (DNAstar, Madison, Wisconsin, USA).

Phylogenetic analyses

Sequences of the 77 *Fusarium* strains studied in this study, and of 98 reference strains downloaded from the databases *Fusarium*-ID (http://www.fusariumdb.org/index.php) and GenBank (https://www.ncbi.nlm.nih.gov/genbank), are listed in Table 1. For each locus, sequences were aligned using MAFFT v. 7 (Katoh et al. 2017), and the alignments were manually adjusted where necessary. The best-fit nucleotide substitution models under the Akaike Information Criterion (AIC) were selected using jModelTest v. 2.1.7 (Posada 2008, Darriba et al. 2012). Alignments derived from this study were deposited in TreeBASE (submission ID 23708), and taxonomic novelties in MycoBank.

Phylogenetic analyses of both individual and combined datasets were performed using Bayesian inference (BI) and Maximum-likelihood (ML) methods. The BI analyses were conducted using MrBayes v. 3.2.1 (Huelsenbeck & Ronquist 2001) following the protocol of Cheng et al. (2015), with optimisation of each locus treated as partitions in combined analyses, based on the Markov Chain Monte Carlo (MCMC) approach (Ronquist et al. 2012). All characters were equally weighted, and gaps were treated as missing data. Stationarity of analysis was determined by examining the standard deviation of split frequencies (< 0.01) and –ln likelihood plots in AWTY (Nylander et al. 2008). Posterior probabilities values over 0.95 were considered significant. ML analysis was conducted using PhyML v. 3.0 (Guindon et al. 2010), with 1 000 bootstrap replicates. The general time reversible model was applied with an invariable gamma-distributed rate variation (GTR+I+G). Bootstrap values over 80 % were considered significant. Both the BI and ML trees were rooted with *Fusarium polyphialidicum* NRRL 13459.

RESULTS

Phylogeny

All five loci employed in this study were amplified with 100 % success rate. The final concatenated alignment included 163 isolates, consisting of 5 108 characters: 507 for ITS, 656 for *EF-1α*, 662 for *CAM*, 1 583 for *RPB1* and 1 700 for *RPB2*. The best nucleotide substitution model for ITS and *RPB1* loci was SYM+I+G, while GTR+I+G was selected for *EF-1α* and *RPB2*, and SYM+G was selected for *CAM.* The topology of multi-locus phylogenetic trees retrieved from ML and BI analyses were congruent (Fig. 1). Two major clades of the FIESC, the *Equiseti* and *Incarnatum* clades, were determined in the multi-locus phylogenetic trees (Fig. 1). The numbers of the FIESC phylogenetic species (1–31) in this study were marked following those defined by O'Donnell et al. (2012) and Villani et al. (2016). Overall, 33 phylogenetic species were recognised in the multi-locus phylogenetic tree (Fig. 1). The 77 isolates obtained in this study represent 12 phylogenetic species spanning the FIESC (Fig. 1), representing two known species (*F. lacertarum* and *F. sulawense*) and nine novel species.

The ITS phylogeny failed to distinguish the two major clades (*Equiseti* and *Incarnatum*), and none of the 33 phylogenetic species could be recognised (Fig. S1a). The *EF-1α* phylogeny was able to distinguish the two major clades, with 21 phylogenetic species resolved (i.e., FIESC 5–14, 19, 20, 23 and 25–32; Fig. S1b). The *CAM* phylogeny was only able to distinguish 18 phylogenetic species (i.e., FIESC 1–8, 10–12, 19, 20, 24, 27, 28, 31 and 33; Fig. S1c). The *RPB1* locus was able to distinguish 21 phylogenetic species (i.e., FIESC 1–8, 13–15, 19–26, 29 and 33; Fig. S1d). The *RPB2* locus provided the best species resolution compared to the other four tested loci, with 25 of the 33 phylogenetic species resolved (1, 3, 5–15, 19, 22–24 and 26–33; Fig. S1e).

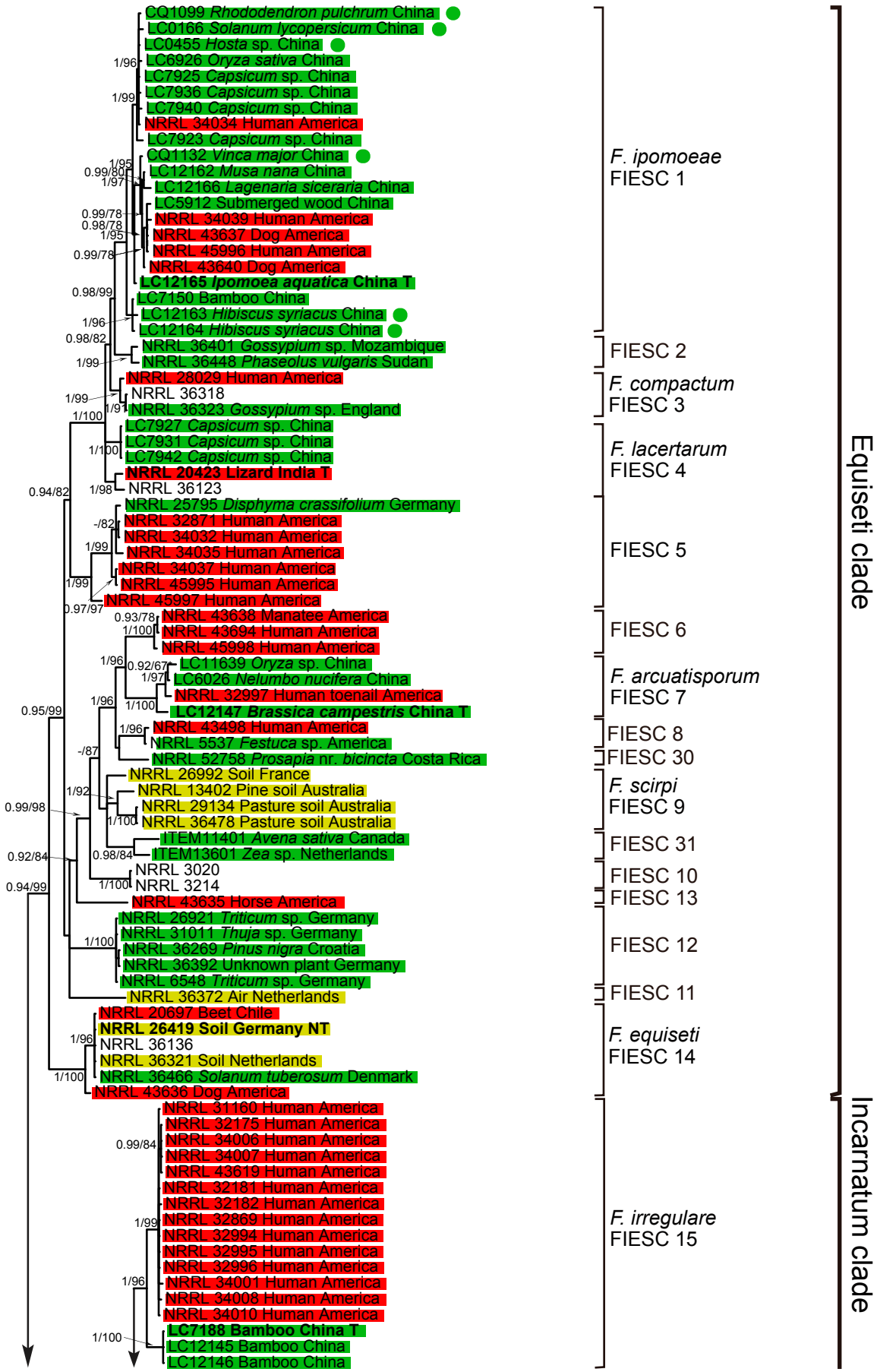

Fig. 1 Fifty percent majority rule consensus tree from a Bayesian analysis based on a five-locus combined dataset (ITS, *EF-1α*, *CAM*, *RPB1* and *RPB2*) showing the phylogenetic relationships of species within the *Fusarium incarnatum-equiseti* species complex (FIESC). The Bayesian posterior probabilities (PP > 0.9) and PhyML Bootstrap support values (BS > 70) are displayed at the nodes (PP/ML). The tree was rooted to *F. polyphialidicum* (NRRL 13459). Ex-type cultures are indicated in **bold** with 'T', and neotype in **bold** with 'NT'. Plant-inhabiting isolates are distinguished by green shading, while human and veterinary isolates by red shading, fungicolous isolates by brown shading, and isolates from environmental habitats by yellow shading. Red stars indicate plant pathogenic isolates. Green dots indicate that isolates are isolated from newly recorded hosts.

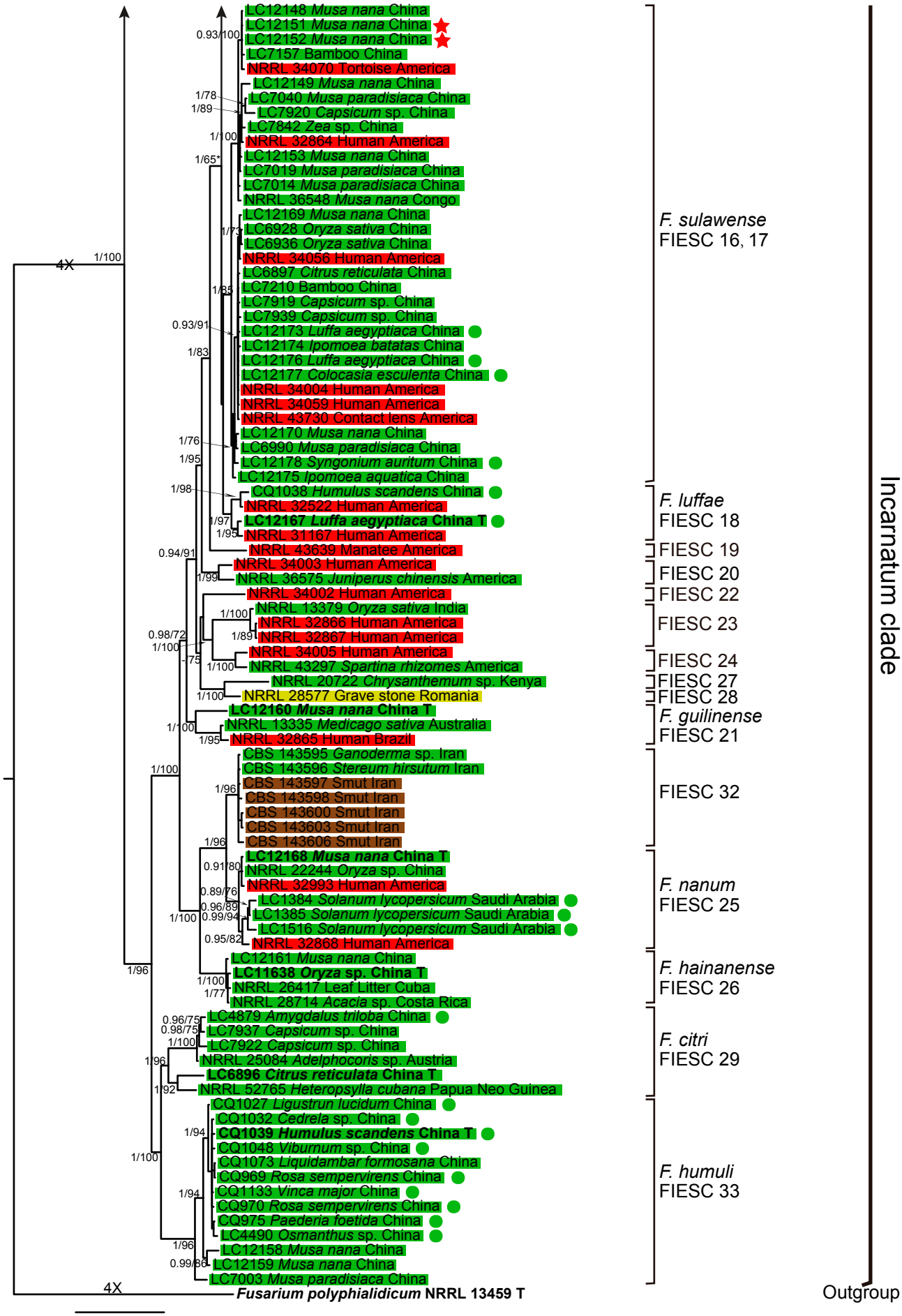
LC12148 Musa nana China
LC12151 Musa nana China
LC12152 Musa nana China
LC7157 Bamboo China
NRRL 34070 Tortoise America
LC12149 Musa nana China
LC7040 Musa paradisiaca China
LC7920 Capsicum sp. China
LC7842 Zea sp. China
NRRL 32864 Human America
LC12153 Musa nana China
LC7019 Musa paradisiaca China
LC7014 Musa paradisiaca China
NRRL 36548 Musa nana Congo
LC12169 Musa nana China
LC6928 Oryza sativa China
LC6936 Oryza sativa China
NRRL 34056 Human America
LC6897 Citrus reticulata China
LC7210 Bamboo China
LC7919 Capsicum sp. China
LC7939 Capsicum sp. China
LC12173 Luffa aegyptiaca China
LC12174 Ipomoea batatas China
LC12176 Luffa aegyptiaca China
LC12177 Colocasia esculenta China
NRRL 34004 Human America
NRRL 34059 Human America
NRRL 43730 Contact lens America
LC12170 Musa nana China
LC6990 Musa paradisiaca China
LC12178 Syngonium auritum China
LC12175 Ipomoea aquatica China
CQ1038 Humulus scandens China
NRRL 32522 Human America
LC12167 Luffa aegyptiaca China T
NRRL 31167 Human America
NRRL 43639 Manatee America
NRRL 34003 Human America
NRRL 36575 Juniperus chinensis America
NRRL 34002 Human America
NRRL 13379 Oryza sativa India
NRRL 32866 Human America
NRRL 32867 Human America
NRRL 34005 Human America
NRRL 43297 Spartina rhizomes America
NRRL 20722 Chrysanthemum sp. Kenya
NRRL 28577 Grave stone Romania
LC12160 Musa nana China T
NRRL 13335 Medicago sativa Australia
NRRL 32865 Human Brazil
CBS 143595 Ganoderma sp. Iran
CBS 143596 Stereum hirsutum Iran
CBS 143597 Smut Iran
CBS 143598 Smut Iran
CBS 143600 Smut Iran
CBS 143603 Smut Iran
CBS 143606 Smut Iran
LC12168 Musa nana China T
NRRL 22244 Oryza sp. China
NRRL 32993 Human America
LC1384 Solanum lycopersicum Saudi Arabia
LC1385 Solanum lycopersicum Saudi Arabia
LC1516 Solanum lycopersicum Saudi Arabia
NRRL 32868 Human America
LC12161 Musa nana China
LC11638 Oryza sp. China T
NRRL 26417 Leaf Litter Cuba
NRRL 28714 Acacia sp. Costa Rica
LC4879 Amygdalus triloba China
LC7937 Capsicum sp. China
LC7922 Capsicum sp. China
NRRL 25084 Adelphocoris sp. Austria
LC6896 Citrus reticulata China T
NRRL 52765 Heteropsylla cubana Papua Neo Guinea
CQ1027 Ligustrun lucidum China
CQ1032 Cedrela sp. China
CQ1039 Humulus scandens China T
CQ1048 Viburnum sp. China
CQ1073 Liquidambar formosana China
CQ969 Rosa sempervirens China
CQ1133 Vinca major China
CQ970 Rosa sempervirens China
CQ975 Paederia foetida China
LC4490 Osmanthus sp. China
LC12158 Musa nana China
LC12159 Musa nana China
LC7003 Musa paradisiaca China
Fusarium polyphialidicum NRRL 13459 T
4X
4X
0.02
F. sulawense
FIESC 16, 17
F. luffae
FIESC 18
FIESC 19
FIESC 20
FIESC 22
FIESC 23
FIESC 24
FIESC 27
FIESC 28
F. guilinense
FIESC 21
FIESC 32
F. nanum
FIESC 25
F. hainanense
FIESC 26
F. citri
FIESC 29
F. humuli
FIESC 33
Incarnatum clade
Outgroup

Fig. 1 (cont.)

Taxonomy

Combining the multi-locus phylogenetic analyses, morphological characteristics and ecological pattern of distribution, we accept 14 species within the FIESC complex, including nine species that are new to science.

Fusarium arcuatisporum M.M. Wang, Qian Chen & L. Cai, *sp. nov.* — MycoBank MB829532; Fig. 2

Etymology. Named after the arcuate shape of the macroconidia.

Typus. China, Hubei Province, from pollen of *Brassica campestris*, Mar. 2016, *Y.Z. Zhao* (HAMS 248034, holotype designated here, dried culture on SNA with carnation leaves; culture ex-type CGMCC3.19493 = LC12147).

Colonies on PDA grown in the dark reaching 4.8–5.3 cm diam after 7 d at 25 °C, slightly raised, aerial mycelia dense, chartreuse (2C6), colony margin undulate, radially striated, pinkish white (9A2); reverse greyish yellow (4C5) in the centre, pinkish white (9A2) at the margin. Colonies on OA grown in the dark reaching 6.2–7.3 cm diam after 7 d at 25 °C, convex, aerial mycelia dense, colony margin entire, pinkish white (9A2); reverse pinkish white (9A2). Colonies on SNA grown in the dark reaching 5.5–5.9 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin erose, white; reverse white. Pigment and odour absent. *Sporodochia* pale orange, present on aerial mycelia on the surface of carnation leaves. *Conidiophores* in sporodochia variable in length, verticillately branched and densely packed, mostly bearing apical whorls of 1–3 monophialides; *sporodochial phialides* subulate to subcylindrical, smooth and thin-walled, hyaline, 7.5–14.5 × 3–6 µm (av. ± SD: 10.6 ± 1.6 × 3.9 ± 0.8 µm). *Sporodochial macroconidia* falcate, slightly curved to dorsiventral curvature, slightly rough, hyaline, apical cell hooked to tapering, basal cell foot-shaped, 5-septate, 29–49.5 × 4–6 µm (av. ± SD: 41 ± 4.9 × 4.7 ± 0.6 µm). *Chlamydospores* abundant, intercalarily or terminal, ellipsoid, globose, smooth, thick-walled, hyaline, 0–2-septate, 4–6.5 × 3.5–5 µm (av. ± SD: 5.1 ± 0.8 × 4.2 ± 0.3 µm).

Additional materials examined. China, Hainan Province, from *Oryza* sp., Mar. 2017, *G.H. Huang* (LC11639); Jiangxi Province, Nanchang, from leaf of *Nelumbo nucifera*, *M.F. Hu* (LC6026).

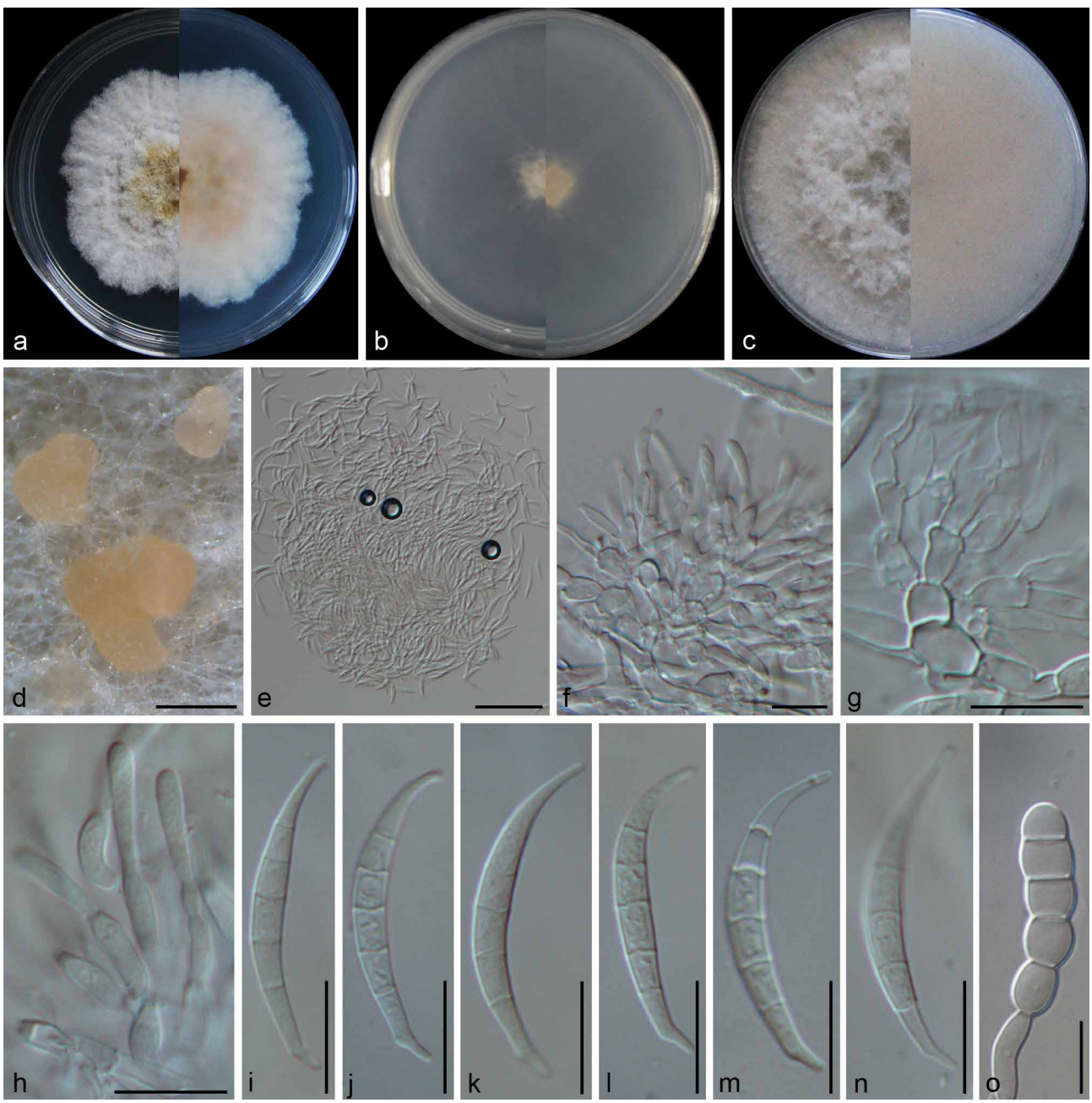

Fig. 2 *Fusarium arcuatisporum* LC12147. a–c. Colonies on PDA, SNA and OA; d–e. sporodochia formed on aerial hyphae on the carnation leaf; f–h. conidiogenous cells form on sporodochia; i–n. macroconidia; o. chlamydospores. — Scale bars: d = 100 µm, e = 50 µm, f–o = 10 µm.

Notes — During the investigation of endophytic fungi from pollen of *Brassica campestris* (colewort), isolate LC12147 was retrieved using the plate dilution method. To our knowledge, this is the first record of FIESC members on colewort. *Fusarium arcuatisporum* is morphologically similar to other species within the *Equiseti* clade with macroconidia having a characteristic tapering apical cell and foot-shaped basal cell (Wollenweber & Reinking 1935, Leslie & Summerell 2006). However, it can easily be distinguished by the arcuate, 5-septate macroconidia. Phylogenetically, *F. arcuatisporum* is closely related to three undescribed phylogenetic species, FIESC 6, 8 and 30 (Fig. 1), but the latter three all lack morphological descriptions. The closest known species to *F. arcuatisporum* is *F. scirpi* (Fig 1), which has 138 bp differences in the five loci sequenced. *Fusarium arcuatisporum* is morphologically distinct from *F. scirpi* based on the number of septa and macroconidial dimensions (5-septate, 29–49.5 × 4–6 µm in *F. arcuatisporum* vs 3–9-septate, usually 6–7-septate, 17–83 × 2.5–6 µm in *F. scirpi*) (Wollenweber & Reinking 1935, Leslie & Summerell 2006). Moreover, microconidia are absent in *F. arcuatisporum*, but present in *F. scirpi*. Ecologically, isolates of *F. arcuatisporum* are isolated from plants in moist and warm regions, as well as from a human toenail. In contrast, *F. scirpi* is more often isolated from soil in arid and semi-arid regions (Leslie & Summerell 2006).

Fusarium citri M.M. Wang, Qian Chen & L. Cai, *sp. nov*. — MycoBank MB829534; Fig. 3

Etymology. Named after the host genus *Citrus*, from which the holotype was isolated.

Typus. China, Hunan Province, from leaf of *Citrus reticulata*, Sept. 2015, *X. Zhou* (HAMS 248036, holotype designated here, dried culture on SNA with carnation leaves, culture ex-type CGMCC3.19467 = LC6896).

Colonies on PDA grown in the dark reaching 5.3–5.7 cm diam after 7 d at 25 °C, flat, aerial mycelia dense, colony margin entire, greyish yellow (1B3); reverse greyish yellow (1B3) in the centre, pale yellow (1A3) at the margin. Colonies on OA grown in the dark reaching 5.9–6.3 cm diam after 7 d at 25 °C, slightly

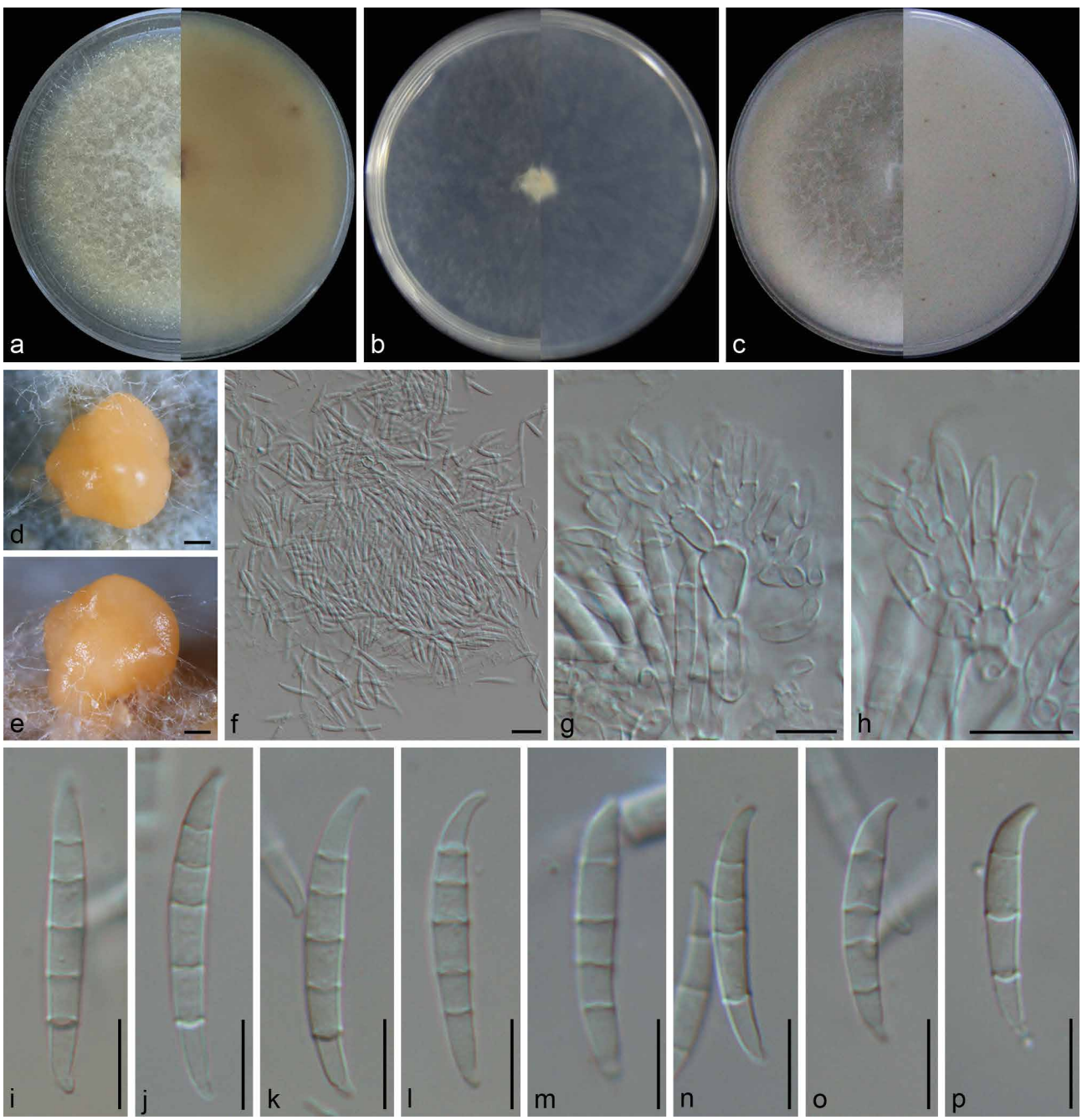

Fig. 3 *Fusarium citri* LC6896. a–c. Colonies on PDA, SNA and OA; d–f. sporodochia formed on the carnation leaf; g–h. conidiogenous cells form on sporodochia; i–p. macroconidia. — Scale bars: d–f = 20 µm, g–p = 10 µm.

raised, aerial mycelia slightly dense, colony margin entire, pinkish white (9A2); reverse pinkish white (9A2). Colonies on SNA grown in the dark reaching 5.5–5.9 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin erose, white; reverse white. Pigment pale brown on PDA, absent on SNA and CLA. Odour absent. *Sporodochia* orange, present on the surface of carnation leaves and agar. *Conidiophores* in sporodochia variable in length, verticillately branched and densely packed, mostly bearing apical whorls of three monophialides; *sporodochial phialides* subulate to subcylindrical, smooth and thin-walled, hyaline, 7.5–11.5 × 2–4 µm (av. ± SD: 9.4 ± 0.9 × 2.9 ± 0.4 µm). *Sporodochial macroconidia* falcate, straight to slightly curved, slightly rough, hyaline, apical cell papillate to hooked, basal cell distinctly notched to foot-shaped, 3–5-septate, 3-septate macroconidia 25–31 × 3.5–5 µm (av. ± SD: 28.9 ± 1.4 × 4 ± 0.3 µm); 4-septate macroconidia 30.5–39 × 3–5.5 µm (av. ± SD: 34.7 ± 1.9 × 4.2 ± 0.4 µm); 5-septate macroconidia 30.5–40.5 × 3–5.5 µm (av. ± SD: 35.3 ± 2.3 × 4.2 ± 0.5 µm). *Microconidia* not observed. *Chlamydospores* not observed.

Additional materials examined. China, Beijing, from *Amygdalus triloba*, Sept. 2012, *X.B. Du* (LC4879); Shandong Province, from *Capsicum* sp., Sept. 2015, *Y.Z. Diao* (LC7922, LC7937).

Notes — Isolates of *Fusarium citri* formed a monophyletic basal lineage within the *Incarnatum* clade, FIESC 29 (Fig. 1). *Fusarium citri* is phylogenetically closest to *F. humuli*, but differs by 182 bp in the five loci dataset. Morphologically, *F. citri* is distinct in the size of its macroconidia (25.5–40.5 × 3–5.5 µm in *F. citri* vs 21–35 × 2–3 µm in *F. humuli*). All 10 isolates of *F. citri* were obtained from plant hosts, suggesting a potential plant-inhabiting preference.

Fusarium compactum (Wollenw.) Raillo, Fungi of the genus Fusarium: 180. 1950

Basionym. *Fusarium scirpi* var. *compactum* Wollenw., Fusaria Autographica Delineata 3: no. 924. 1930.

Synonym. *Fusarium equiseti* var. *compactum* (Wollenw.) Joffe, Pl. & Soil 38: 440. 1973.

Description — See Wollenweber & Reinking (1935).

Notes — *Fusarium compactum* was initially proposed as a new name for *F. scirpi* var. *compactum* in Raillo (1950) based on the original morphological description provided by Wollenweber & Reinking (1935). Isolate NRRL 36323 is a good voucher isolate of *F. compactum*, as it matched the original description of *F. compactum* as well as host, location, collector, and collection time. Based on macroconidial morphology, this species resembles *F. equiseti* (Wollenweber & Reinking 1935, Leslie & Summerell 2006). However, the shape of the apical cell can distinguish the two species (needle-like in *F. compactum* vs whip-like in *F. equiseti*; Wollenweber & Reinking 1935, Leslie & Summerell 2006). In addition, *F. compactum* is phylogenetically distinct from *F. equiseti* (Fig. 1).

Fusarium equiseti (Corda) Sacc., Syll. Fung. (Abellini) 4: 707. 1886

Basionym. *Selenosporium equiseti* Corda 1838, Icon. Fungorum (Prague) 2: 7. 1838.

Synonyms. *Fusarium falcatum* Appel & Wollenw., Arb. Kaiserl. Biol. Anst. Ld.- u. Forstw. 8: 184. 1910.

Fusoma pallidum Bonord., Abh. Naturf. Ges. Halle 8: 87. 1864.

Description — See Wollenweber & Reinking (1935).

Notes — A number of species have been historically treated as synonyms of *Fusarium equiseti*, for instance *F. falcatum*, *F. falcatum* var. *fuscum*, *F. mucronatum*, *Fusisporium ossicola*, *Fusoma ossicolum* and *Fusoma pallidum* (Wollenweber & Reinking 1935). *Fusarium falcatum* and *Fusoma pallidum* are indistinguishable from *F. equiseti* based on original morphological descriptions (Bonorden 1864, Appel & Wollenweber 1910, Wollenweber & Reinking 1935), thus have been listed as synonyms of *F. equiseti* (Wollenweber & Reinking 1935). *Fusarium equiseti* differs from *F. falcatum* var. *fuscum* in the shape of the macroconidia (fusiform to arcuate in *F. equiseti* vs ellipsoidal to parabolic dorsally curved in *F. falcatum* var. *fuscum*; Sherbakoff 1915), and from *Fusisporium ossicola* in the shape of the apical cell of the macroconidia (uncinate in *Fusis. ossicola* vs tapering to whip-like in *F. equiseti*; Berkeley 1875). *Fusarium equiseti* is a cosmopolitan soil inhabitant, as well as pathogen of plants, animals and humans (Leslie & Summerell 2006). *Fusarium equiseti* was often confused with several other species in morphology, such as *F. compactum*, *F. ipomoeae*, *F. longipes* and *F. scirpi*, based on the spindle-shaped macroconidia (Wollenweber & Reinking 1935, Leslie & Summerell 2006), but could be differentiated from *F. compactum* by the shape of the apical cell of its macroconidia (discussed in the notes of *F. compactum*), from *F. ipomoeae* by the shape of the apical cell and macroconidial septation (tapering to whip-like apical cell, 3–12-septate, usually 5–7-septate in *F. equiseti* vs hooked to tapering apical cell, 3–5-septate in *F. ipomoeae*), from *F. scirpi* by the absence of microconidia (present in *F. scirpi*), from *F. longipes* by the pigment formation on PDA (brown in *F. equiseti* vs red in *F. longipes*; Wollenweber & Reinking 1935, Leslie & Summerell 2006).

Fusarium guilinense M.M. Wang, Qian Chen & L. Cai, *sp. nov*. — MycoBank MB829535; Fig. 4

Etymology. Named after the city, Guilin, where the holotype was collected.

Typus. China, Guangxi Province, Guilin, from leaf of *Musa nana*, Sept. 2016, *Y.Z. Diao* (HAMS 248037, holotype designated here, dried culture on SNA with carnation leaves, culture ex-type CGMCC3.19495 = LC12160).

Colonies on PDA grown in the dark reaching 5.3–5.7 cm diam after 7 d at 25 °C, convex, aerial mycelia dense, yellowish grey (2D2), colony margin undulate, white; reverse yellowish grey (2C2) in the centre, white at the margin. Colonies on OA grown in the dark reaching 5.7–6.3 cm diam after 7 d at 25 °C, convex, aerial mycelia dense, colony margin entire, pinkish white (9A2); reverse pinkish white (9A2). Colonies on SNA grown in the dark reaching 6.7–7.5 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin undulate, white; reverse white. Pigment and odour absent. *Sporodochia* not observed. *Conidiophores* reduced to monophialides, on the aerial mycelia, subulate to subcylindrical, smooth and thin-walled, hyaline, 11.5–13 × 2.5–3 µm (av. ± SD: 19.8 ± 3 × 4.9 ± 0.2 µm). *Macroconidia* falcate, slender, straight to curved, smooth to slightly rough, hyaline, apical cell blunt or hooked, basal cell barely to distinctly notched, 3-septate, 20–39.5 × 3–4 µm (av. ± SD: 30 ± 5.3 × 3.6 ± 0.4 µm); *microconidia* oval, smooth to slightly rough, hyaline, 1-septate, 8–13.5 × 3–4 µm (av. ± SD: 10.4 ± 1.4 × 3.4 ± 0.3 µm). *Chlamydospores* not observed.

Notes — *Fusarium guilinense* is morphologically similar to *F. luffae* and *F. nanum* based on the absence of sporodochia on CLA, but distinct from the latter two in conidiophore morphology (monophialides in *F. guilinense* vs polyphialides in *F. luffae* and *F. nanum*). *Fusarium guilinense* can also be distinguished from *F. luffae* by the septation and shape of the basal cell of its macroconidia (3-septate, barely to distinctly notched basal cell in *F. guilinense* vs 3–5-septate, barely notched basal cell in *F. luffae*), and from *F. nanum* by the shape of the apical cell of its macroconidia (blunt or hooked apical cell in *F. guilinense* vs blunt to papillate apical cell in *F. nanum*). *Fusarium guilinense* is also distinguished from *F. incarnatum* by the septation

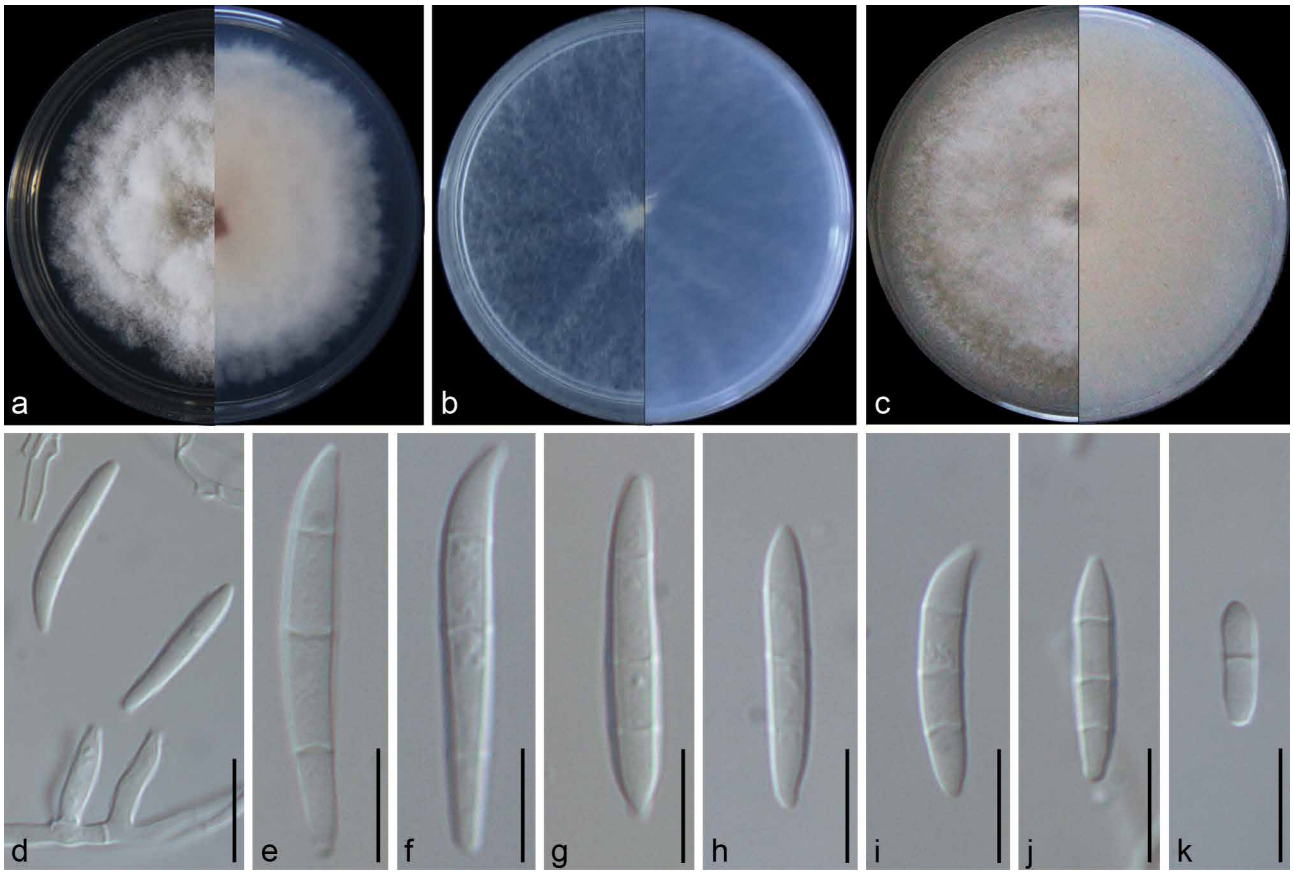

Fig. 4 *Fusarium guilinense* LC12160. a–c. Colonies on PDA, SNA and OA; d. conidiogenous cells form on aerial hyphae; e–k. macroconidia. — Scale bars: d–k = 10 µm.

Fig. 5 *Fusarium hainanense* LC11638. a–c. Colonies on PDA, SNA and OA; d–g. conidiogenous cells form on aerial hyphae; h–k. macroconidia. — Scale bars: d–o = 10 µm.

and length of its macroconidia (3-septate, and 20–39.5 µm in *F. guilinense* vs 3–5-septate, rarely seven, and 35–45 µm in *F. incarnatum*). Comparing with other species recorded from *Musa* spp., *F. guilinense* differs from *F. musae* and *F. musarum* in the formation of macroconidia (Marasas et al. 1998, Van Hove et al. 2011), from *F. semitectum* in the shape of macroconidia (falcate, slender in *F. guilinense* vs oblongo-clavate in *F. semitectum*), and from 11 other species in the *F. oxysporum* species complex) in the absence of sporodochia on CLA (Maryani et al. 2019a).

Fusarium hainanense M.M. Wang, Qian Chen & L. Cai, *sp. nov*. — MycoBank MB829536; Fig. 5

Etymology. Named after Hainan Province, the location from which the holotype was collected.

Typus. China, Hainan Province, from stem of *Oryza* sp., Mar. 2016, *G.H. Huang* (HAMS 248038, holotype designated here, dried culture on SNA with carnation leaves, culture ex-type CGMCC3.19478 = LC11638).

Colonies on PDA grown in the dark reaching 5.1–5.6 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, pale orange (5A3), colony margin lobate, white; reverse pale orange (5A3) in the centre, white at the margin. Colonies on OA grown in the dark reaching 5.4–6.3 cm diam after 7 d at 25 °C, crateriform, aerial mycelia scant, colony margin entire, white; reverse white. Colonies on SNA grown in the dark reaching 5.4–5.7 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin undulate, white; reverse white. Pigment and odour absent. *Sporodochia* not observed. *Conidiophores* on the aerial mycelia variable in length; *monophialides* subulate to subcylindrical, smooth and thin-walled, hyaline, variable in length; *polyphialides* smooth and thin-walled, hyaline, with two conidiogenous loci, 20–22.5 × 2–3 µm (av. ± SD: 21.5 ± 0.3 × 2.4 ± 0.5 µm). *Macroconidia* falcate, fusiform, straight to slightly curved, slightly rough, hyaline, sometimes with constricted septa, apical cell blunt to papillate, basal cell barely to distinctly notched, 1- or 3-septate; 1-septate macroconidia 18–22.5 × 3–4 µm (av. ± SD: 20.5 ± 1.4 × 3.7 ± 0.3 µm); 3-septate macroconidia 22–33 × 2.5–5 µm

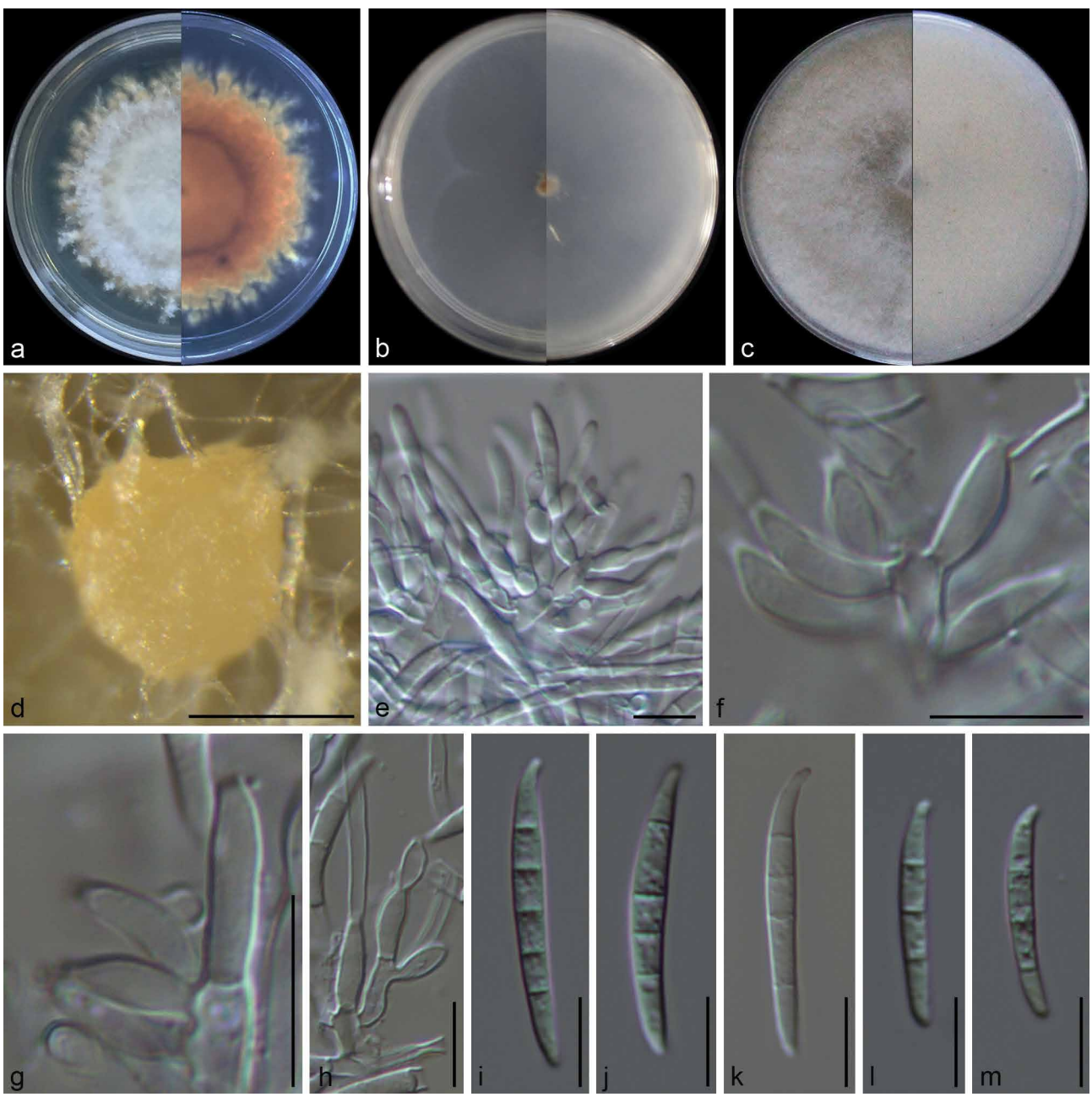

Fig. 6 *Fusarium humuli* CQ1039. a–c. Colonies on PDA, SNA and OA; d–e. sporodochia formed on aerial hyphae; f–h. conidiogenous cells form on sporodochia; i–m. macroconidia. — Scale bars: d = 100 µm, e–m = 10 µm.

(av. ± SD: 27.5 ± 3.6 × 2.7 ± 0.7 µm). *Microconidia* not observed. *Chlamydospores* not observed.

Additional material examined. China, Guangxi Province, Chongzuo, from leaf of *Musa nana*, Aug. 2016, *Y.Z. Diao* (LC12161).

Notes — The type specimen of *F. hainanense* was isolated from the stem of a healthy rice plant. Since all four isolates of *F. hainanense* in this study were collected from tropical or subtropical regions (NRRL 26417 from Cuba, NRRL 28714 from Costa Rica, LC11638 and LC12161 from Hainan and Guangxi Provinces in China, respectively), this species is regarded as a tropical or subtropical species in the genus *Fusarium*. Phylogenetically, *F. hainanense* (FIESC 26) is closest to *F. nanum* (FIESC 25) (Fig. 1), but differs from the latter by 221 bp for the five loci used.

Fusarium humuli M.M. Wang, Qian Chen & L. Cai, *sp. nov*. — MycoBank MB829537; Fig. 6

Etymology. Named after the host genus, *Humulus*, from which the holotype was isolated.

Typus. China, Jiangsu Province, from leaf of *Humulus scandens*, Nov. 2017, *Q. Chen* (HAMS 248039, holotype designated here, dried culture on SNA with carnation leaves, culture ex-type CGMCC3.19374 = CQ1039).

Colonies on PDA grown in the dark reaching 5.1–5.3 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, white, colony margin lobate, white; reverse brownish yellow (5C8) in the centre, white at the margin. Colonies on OA grown in the dark reaching 5.4–6.1 cm diam after 7 d at 25 °C, flat, aerial mycelia dense, colony margin entire, white; reverse white. Colonies on SNA grown in the dark reaching 5.3–5.6 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin undulate, white; reverse white. Pigment and odour absent. *Sporodochia* pale orange, present on aerial hyphae and agar. *Conidiophores* in sporodochia variable in length, verticillately branched and densely packed, bearing apical whorls of 3–7 monophialides; *sporodochial phialides* subulate to subcylindrical, smooth and thin-walled, hyaline, 6.3–11.9 × 2–3.4 µm (av. ± SD: 8.7 ± 2.4 × 3.1 ± 0.9 µm). *Sporodochial macroconidia* falcate, slender, straight to slightly curved, slightly rough, hyaline, apical cell hooked, basal cell barely to distinctly notched, 3–5-septate; 3-septate macroconidia 21–23.5 × 2–2.5 µm (av. ± SD: 22.5 ± 0.9 × 2.3 ± 0.3 µm); 4-septate macroconidia 28–33 × 2–3 µm (av. ± SD: 27.5 ± 1.6 × 2.7 ± 0.7 µm); 5-septate macroconidia 30–35 × 2.5–3 µm (av. ± SD: 32.5 ± 2.4 × 2.9 ± 0.3 µm). *Microconidia* not observed. *Chlamydospores* not observed.

Additional materials examined. China, Guangdong Province, Guangzhou, from leaf of *M. nana*, June 2017, *M.M. Wang* (LC12158, LC12159); Hainan Province, from *M. paradisiaca*, Dec. 2015, *F.J. Liu* (LC7003); Jiangsu Province, from leaf of *Ligustrum lucidum*, Nov. 2017, *Q. Chen* (CQ1027); ibid., from leaf of *Cedrela* sp., Nov. 2017, *Q. Chen* (CQ1032); ibid., from leaf of *Viburnum* sp., Nov. 2017, *Q. Chen* (CQ1048); ibid., from leaf of *Liquidambar formosana*, Nov. 2017, *Q. Chen* (CQ1073); ibid., from leaf of *Rosa sempervirens*, Nov. 2017, *Q. Chen* (CQ969, CQ970); ibid., from leaf of *Vinca major*, Nov. 2017, *Q. Chen* (CQ1133); ibid., from leaf of *Paederia foetida*, Nov. 2017, *Q. Chen* (CQ975); Jiangxi Province, from *Osmanthus* sp., Sept. 2013, *Y.H. Gao, N. Zhou & Y. Zhang* (LC4490).

Notes — Phylogenetically *F. humuli* represents a novel clade within the FIESC, named here FIESC 33, closely related to *F. citri*. The two species differ by 182 bp in the five loci used. Morphologically, the two species are distinguished by the size of their macroconidia (25.5–40.5 × 3–5.5 µm in *F. citri* vs 21–35 × 2–3 µm in *F. humuli*).

Fusarium ipomoeae M.M. Wang, Qian Chen & L. Cai, *sp. nov*. — MycoBank MB829538; Fig. 7

Etymology. Named after the host genus, *Ipomoea*, from which the holotype was isolated.

Typus. China, Fujian Province, from leaf of *Ipomoea aquatica*, Aug. 2016, *L. Cai* (HAMS 248040, holotype designated here, dried culture on SNA with carnation leaves, culture ex-type CGMCC3.19496 = LC12165).

Colonies on PDA grown in the dark reaching 5.3–5.7 cm diam after 7 d at 25 °C, convex, aerial mycelia dense, chartreuse (2C6), colony margin lobate, pinkish white (9A2); reverse greyish orange (5B4) in the centre, pinkish white (9A2) at the margin. Colonies on OA grown in the dark reaching 5.2–6.3 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin entire, white; reverse white. Colonies on SNA grown in the dark reaching 5.1–5.6 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin lobate, white; reverse white. Pigment and odour absent. *Sporodochia* pale orange, present on surface of carnation leaves and agar. *Conidiophores* in sporodochia variable in length, verticillately branched and densely packed, bearing apical whorls of 3–5 monophialides; *sporodochial phialides* subulate to subcylindrical, smooth and thin-walled, hyaline, 8–15 × 2–4 µm (av. ± SD: 10.9 ± 1.6 × 3.5 ± 0.5 µm). *Sporodochial macroconidia* with dorsiventral curvature, smooth, hyaline, apical cell hooked to tapering, basal cell foot-shaped, 3–5-septate; 3-septate macroconidia 26.5–36 × 3–3.5 µm (av. ± SD: 32.4 ± 4.2 × 3.3 ± 0.2 µm); 4-septate macroconidia 36–38.5 × 2–4 µm (av. ± SD: 37.1 ± 0.9 × 3.1 ± 0.6 µm); 5-septate macroconidia 37.5–57 × 2.5–5 µm (av. ± SD: 44.7 ± 3.8 × 3.6 ± 0.6 µm). *Microconidia* not observed. *Chlamydospores* not observed.

Additional materials examined. China, Guangxi Province, Liuzhou, from leaf of *M. nana*, June 2017, *M.M. Wang* (LC12162); Beijing, from fruit of *Solanum lycopersicum*, unknown, *L. Cai* (LC0166); Beijing, from *Hosta* sp., unknown, *F. Liu* (LC0455); Fujian Province, from *Hibiscus syriacus*, Aug. 2016, *L. Cai* (LC12163, LC12164); Fujian Province, from *Lagenaria siceraria*, Aug. 2016, *L. Cai* (LC12166); Hubei Province, from *Oryza sativa*, Sept. 2015, *X. Zhou* (LC6926); Jiangsu Province, from leaf of *Rhododendron pulchrum*, Nov. 2017, *Q. Chen* (CQ1099); ibid., from leaf of *Vinca major*, Nov. 2017, *Q. Chen* (CQ1132); Jiangxi Province, from submerged wood, July 2014, *J.B. Zhang* (LC5912); Jiangxi Province, from bamboo, July 2016, *J.E. Huang* (LC7150); Shandong Province, from *Capsicum* sp., Sept. 2015, *Y.Z. Diao* (LC7923, LC7925, LC7936), *J.Y. Wang* (LC7940).

Notes — Wollenweber (1914) introduced a novel species isolated from *Ipomoae batatas* in the USA as *Fusarium caudatum*. This species was later treated as a synonym of *F. scirpi* var. *caudatum* by Wollenweber (1930). Based on the original morphological description, *F. caudatum* could be distinguished from *F. ipomoeae* by the septation and length of its macroconidia (5-septate, 40–80 µm in *F. caudatum* vs 3–5-septate, 26–57 µm in *F. ipomoeae*; Wollenweber 1914). *Fusarium ipomoeae* is morphologically similar to *F. compactum* and *F. equiseti* based on its macroconidial dimensions, but distinct from the latter two species in pigmentation of the colony on PDA (pigment absent in *F. ipomoeae* vs brown in *F. compactum*, and brown with sometimes dark brown spots or flecks in *F. equiseti*; Wollenweber & Reinking 1935, Leslie & Summerell 2006). Based on the present phylogeny, *F. ipomoeae* (FIESC 1) is distinct from *F. compactum* (FIESC 3) and *F. equiseti* (FIESC 14; Fig. 1). *Fusarium ipomoeae* is phylogenetically closest to FIESC 2, but differs by 58 bp for the five loci used. Since a morphological description is unavailable for FIESC 2, this clade cannot be discussed in detail at present.

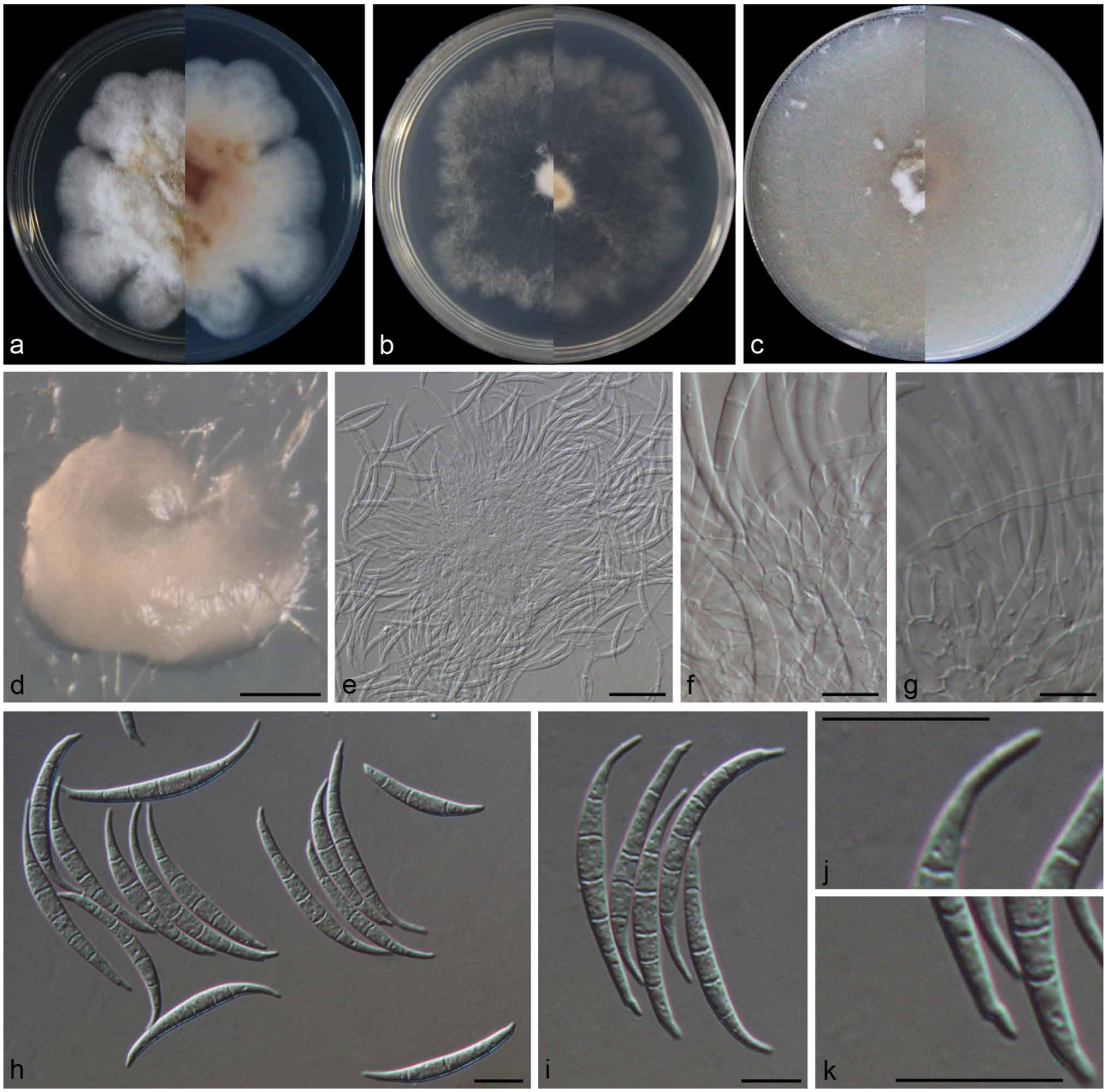

Fig. 7 *Fusarium ipomoeae* LC12165. a–c. Colonies on PDA, SNA and OA; d–e. sporodochia formed on agar near the carnation leaf; f–g. conidiogenous cells form on sporodochia; h–k. macroconidia. — Scale bars: d–e = 50 µm, f–k = 10 µm.

Fusarium irregulare M.M. Wang, Qian Chen & L. Cai, *sp. nov*. — MycoBank MB829539; Fig. 8

Etymology. Named after the irregular shape of its macroconidia.

Typus. China, Guangdong Province, from bamboo, July 2016, *L. Cai* (HAMS 248041, holotype designated here, dried culture on SNA with carnation leaves, culture ex-type CGMCC3.19489 = LC7188).

Colonies on PDA grown in the dark reaching 5.3–5.9 cm diam after 7 d at 25 °C, convex, aerial mycelia dense, colony margin entire, yellowish white (3A2); reverse light orange (6A4) in the centre, yellowish white (3A2) at the margin. Colonies on OA grown in the dark reaching 6.7–7.3 cm diam after 7 d at 25 °C, convex, aerial mycelia dense, colony margin entire, pinkish white (9A2); reverse pinkish white (9A2). Colonies on SNA grown in the dark reaching 5.5–5.9 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin erose, white; reverse white. Pigment pale brown on PDA, absent on SNA. Odour absent. *Sporodochia* not observed. *Conidiophores* in the aerial mycelia variable in length, proliferating percurrently, verticillately branched; *monophialides* subulate to subcylindrical, smooth and thin-walled, hyaline, 13.5–22.5 × 2–4 µm (av. ± SD: 17.2 ± 4 × 3.1 ± 0.7 µm). *Macroconidia* falcate, straight to slightly curved, slightly rough, hyaline, apical cell blunt, basal cell barely notched, sometime with elongate or even whip-like apical or basal cell, mostly 3-septate, 16–38.5 × 3–5 µm (av. ± SD: 25.8 ± 5.8 × 3.8 ± 0.6 µm). *Microconidia* not observed. *Chlamydospores* not observed.

Additional material examined. China, Guangdong Province, from bamboo, July 2016, *L. Cai* (LC12145, LC12146).

Notes — *Fusarium irregulare* represents FIESC 15 in the *Incarnatum* clade. Morphologically, it could produce macroconidia with elongate, even whip-like, apical or basal cells, which is distinct from other *Incarnatum* species with blunt, papillate to hooked apical cells and barely notched to foot-shaped basal cells. *Fusarium irregulare* is similar to *F. aywerte*, *F. equiseti* and *F. longipes* in bearing a whip-like cell in the macroconidia, but can be distinguished from *F. equiseti* in producing falcate, straight to slightly curved macroconidia (dorsiventral curvature in *F. equiseti*), and from the other two species in the septation of

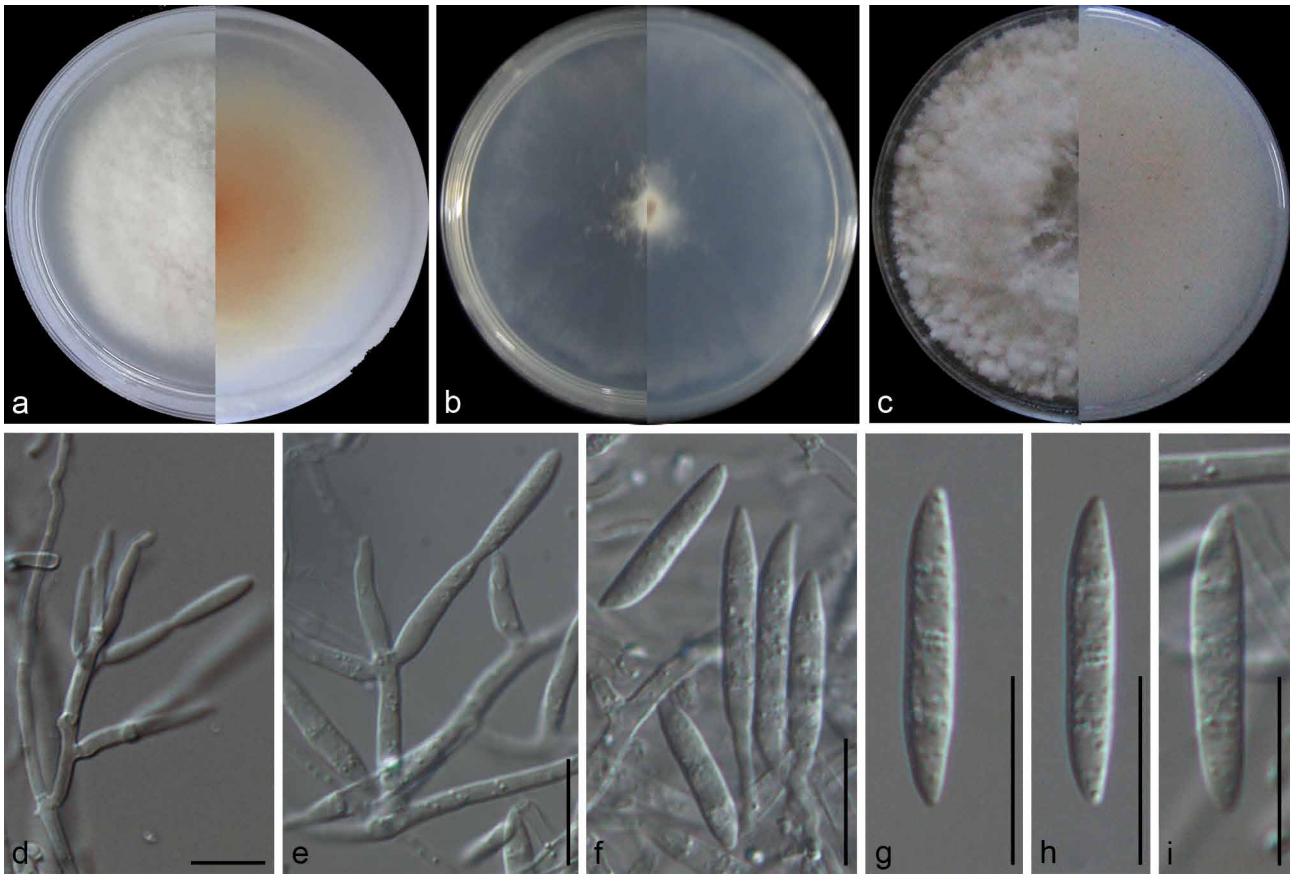

Fig. 8 *Fusarium irregulare* LC7188. a–c. Colonies on PDA, SNA and OA; d–e. conidiophore formed on aerial hyphae; f–i. macroconidia. — Scale bars: d–j = 10 µm.

its macroconidia (mostly 3-septate in *F. irregulare* vs 6–8-septate in *F. aywerte* and 5–7-septate in *F. longipes*; Wollenweber & Reinking 1935, Benyon et al. 2000). Phylogenetically, *F. aywerte* belongs to the *F. chlamydosporum* species complex (Laurence et al. 2016), while *F. longipes* belongs to the *F. sambucinum* species complex (Sandoval-Denis et al. 2018b).

Fusarium lacertarum Subrahm. (as '*laceratum*'), Mykosen 26: 478. 1983

Description — See Subrahmanyam (1983).

Materials examined. China, Shandong Province, from *Capsicum* sp., Sept. 2015, *Y.Z. Diao* (LC7927, LC7931, LC7942).

Notes — *Fusarium lacertarum* is the only species recorded in the FIESC which has been isolated from a snake (Subrahmanyam 1983). It is similar to *F. flocciforme* in morphological characters, but differentiated from the latter in producing longer conidia (6.6–30.8 µm in *F. lacertarum* vs 8.3–14.9 µm in *F. flocciforme*; Subrahmanyam 1983). Phylogenetically, *F. flocciforme* is located in the *F. tricinctum* species complex (FTSC), which forms a distinct lineage from the FIESC (Sandoval-Denis et al. 2018a).

Fusarium luffae M.M. Wang, Qian Chen & L. Cai, *sp. nov*. — MycoBank MB829540; Fig. 9

Etymology. Name reflects the host genus *Luffa* from which it was isolated.

Typus. China, Fujian Province, from *Luffa aegyptiaca*, Aug. 2016, *L. Cai* (HAMS 248042, holotype designated here, dried culture on SNA with carnation leaves, culture ex-type CGMCC3.19497 = LC12167).

Colonies on PDA grown in the dark reaching 5.3–5.7 cm diam after 7 d at 25 °C, convex, aerial mycelia dense, wax yellow (3B5), colony margin erose, white; reverse pale orange (6A3) in the centre, white at the margin. Colonies on OA grown in the dark reaching 6.2–7.3 cm diam after 7 d at 25 °C, raised, aerial mycelia dense, greyish yellow (1B4), colony margin entire, white; reverse white. Colonies on SNA grown in the dark reaching 4.7–5.2 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin lobate, white; reverse white. Pigment and odour absent. *Sporodochia* not observed. *Conidiophores* on the aerial mycelia variable in length, irregularly branched; *polyphialides* subulate to subcylindrical, smooth and thin-walled, hyaline, with 3–5 conidiogenous loci, 15–24 × 4.7–5.1 µm (av. ± SD: 19.8 ± 3 × 4.9 ± 0.2 µm). *Macroconidia* falcate, slender, straight to curved, smooth to slightly rough, hyaline, apical cell blunt or hooked, basal cell barely notched, 3–5-septate; 3-septate macroconidia 26.5–29.5 × 4–4.5 µm (av. ± SD: 28 ± 1.1 × 4.1 ± 0.1 µm); 4-septate macroconidia 30–32 × 4–4.5 µm (av. ± SD: 31.8 ± 1.2 × 4.5 ± 0.1 µm); 5-septate macroconidia 35–46 × 4–5 µm (av. ± SD: 40.3 ± 2.9 × 4.4 ± 0.3 µm). *Microconidia* not observed. *Chlamydospores* not observed.

Additional material examined. China, Jiangsu Province, from leaf of *Humulus scandens*, Nov. 2017, *Q. Chen* (CQ1038).

Notes — Phylogenetically, *F. luffae* represents FIESC 18, and is closely related to *F. sulawense* (FIESC 16, 17). Morphologically, this species can easily be distinguished from the latter two by the formation of polyphialides and the absence of sporodochia on CLA.

Fusarium nanum M.M. Wang, Qian Chen & L. Cai, *sp. nov*. — MycoBank MB829541; Fig. 10

Etymology. Name reflects the host species *Musa nana,* from which it was isolated.

Typus. China, Guangxi Province, Guilin, from leaf of *Musa nana*, Aug. 2016, *Y.Z. Diao* (HAMS 248043, holotype designated here, dried culture on SNA with carnation leaves, culture ex-type CGMCC3.19498 = LC12168).

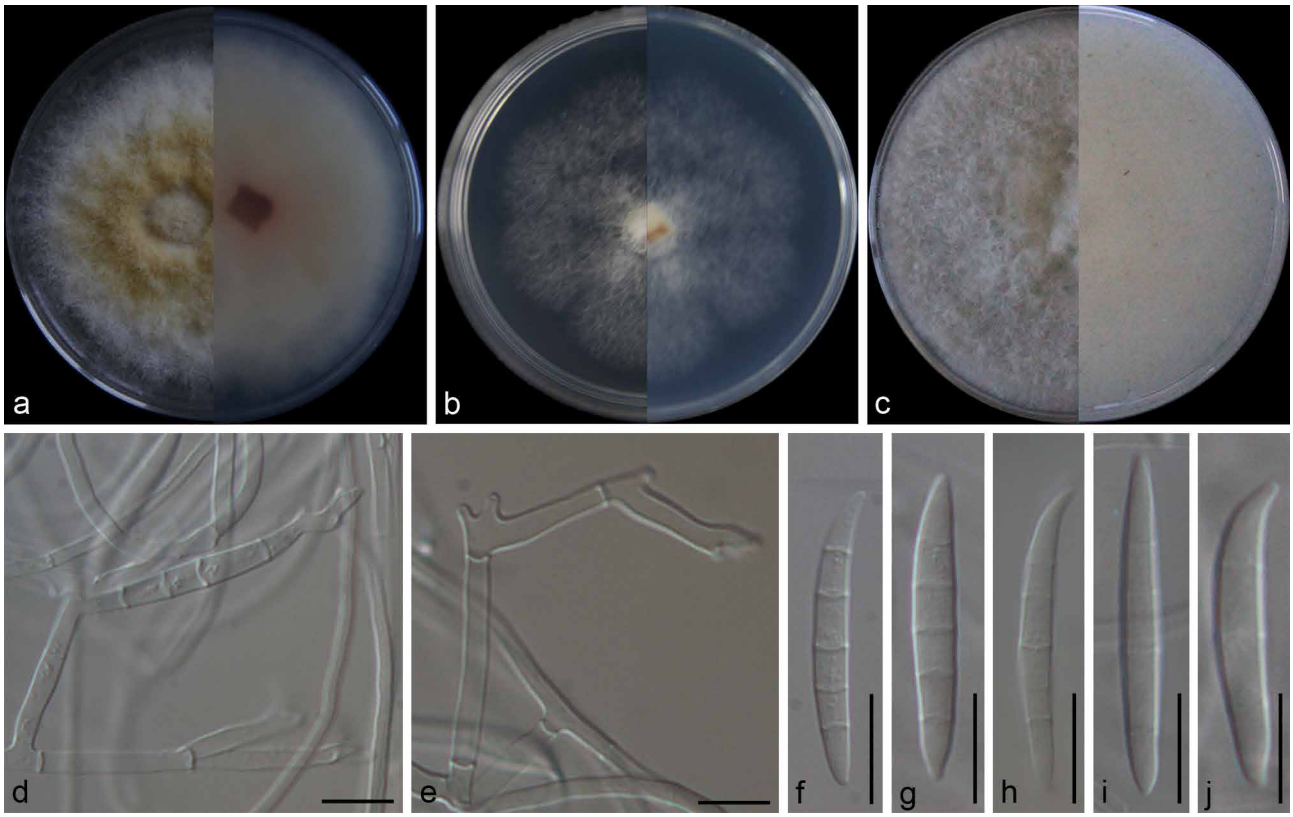

Fig. 9 *Fusarium luffae* LC12167. a–c. Colonies on PDA, SNA and OA; d–e. conidiophores formed on aerial hyphae; f–j. macroconidia. — Scale bars: d–j = 10 µm.

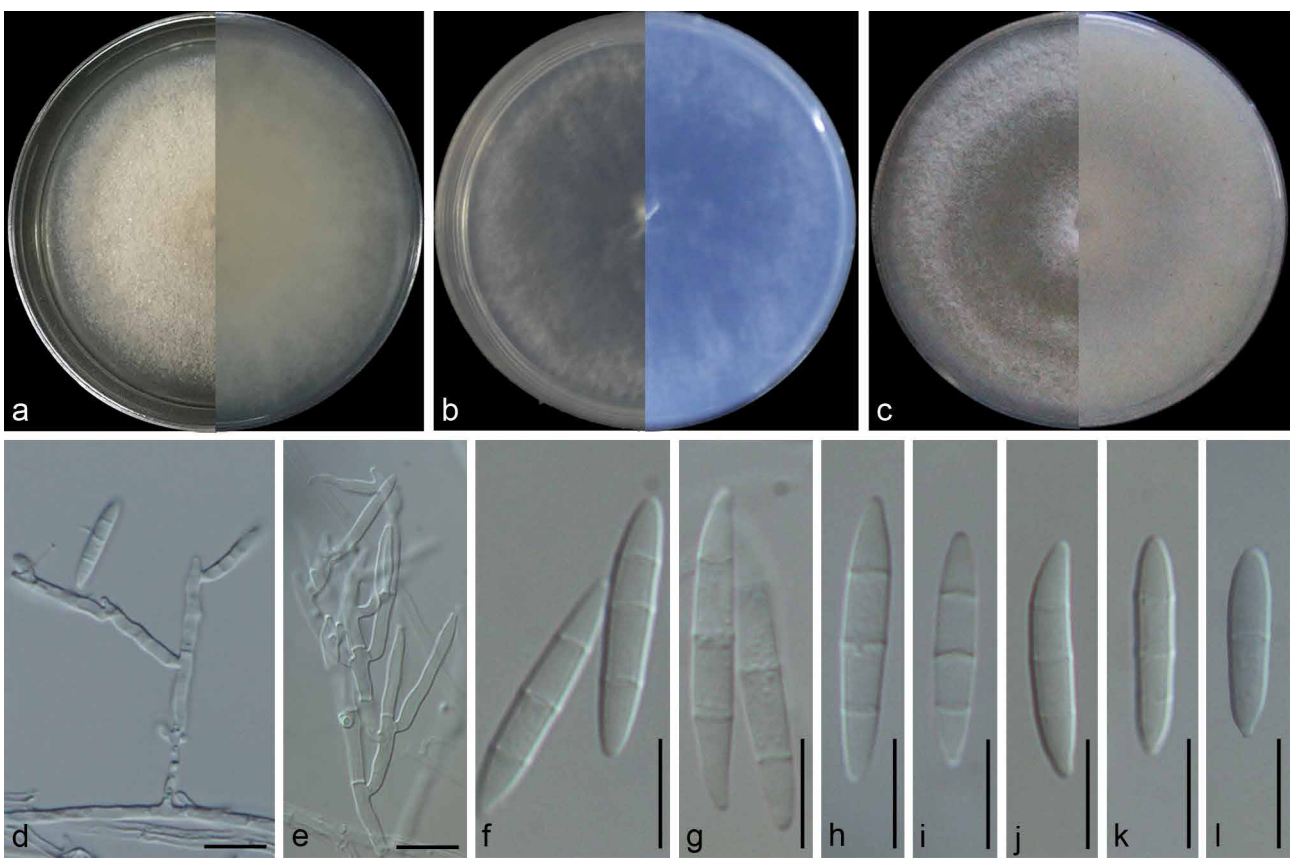

Fig. 10 *Fusarium nanum* LC12168. a–c. Colonies on PDA, SNA and OA; d–e. conidiophores formed on aerial hyphae; f–l. macroconidia. — Scale bars: d–l = 10 µm.

Colonies on PDA grown in the dark reaching 5.1–5.6 cm diam after 7 d at 25 °C, flat, aerial mycelia dense, colony margin entire, cream yellow (4A3); reverse yellowish white (4A2) in the centre, white at the margin. Colonies on OA grown in the dark reaching 6.2–7.3 cm diam after 7 d at 25 °C, crateriform, aerial mycelia scant, colony margin entire, pinkish white (9A2); reverse white. Colonies on SNA grown in the dark reaching 5.4–5.7 cm diam after 7 d at 25 °C, flat, aerial mycelia scant, colony margin erose, white; reverse white. Pigment and odour absent. *Sporodochia* not observed. *Conidiophores* on the aerial mycelia variable in length, proliferating percurrently, verticillately branched; *monophialides* subulate to subcylindrical, smooth and thin-walled, hyaline, 15–31.5 × 3.1–4.4 µm (av. ± SD: 21.2 ± 4.2 × 3.8 ± 0.4 µm); *polyphialides* smooth and thin-walled, hyaline, with two or more conidiogenous loci, variable in length. *Macroconidia* falcate, straight to slightly curved, smooth to slightly rough, hyaline, apical cell blunt to papillate, basal cell barely to distinctly notched, 3-septate, 20.5–32 × 3–5 µm (av. ± SD: 25.1 ± 3.6 × 3.9 ± 0.4 µm). *Microconodia* obovoid, smooth to slightly rough, hyaline, 1- or 3-septate; 1-septate macroconidia 11–15.5 × 3–4 µm (av. ± SD: 13.4 ± 1.4 × 3.9 ± 0.5 µm); 3-septate macroconidia 19–29.5 × 3–5 µm (av. ± SD: 24.3 ± 3.2 × 3.8 ± 0.3 µm). *Chlamydospores* not observed.

Additional materials examined. Saudi Arabia, from *Solanum lycopersicum*, collector and collection date unknown (LC1384, LC1385, LC1516).

Notes — *Fusarium nanum* represents FIESC 25 in the *Incarnatum* clade. Phylogenetically, *F. nanum* is closely related to *F. hainanense*, but differs from the latter by 164 bp for the five loci used in this study. The macroconidia of *F. nanum* are similar to *F. guilinense*, but can be distinguished from the latter species by the septation and shape of the apical cell of the macroconidia (2–3-septate, blunt to papillate apical cell in *F. nanum* vs 3-septate, blunt or hooked apical cell in *F. guilinense*). Morphologically, *F. nanum* is distinct from *F. semitectum* based on macroconidial septation (3-septate in *F. nanum* vs 0–7-septate in *F. semitectum*).

Fusarium scirpi Lambotte & Fautrey, Rev. Mycol. (Toulouse) 16 (no. 63): 111. 1894

Synonyms. *Fusoma helminthosporii* Corda, Icon. Fungorum (Prague) 1: 7. 1837.

Fusisporium chenopodinum Thüm., Mycoth. Univ., cent. 14: no. 1378. 1879.

Fusarium chenopodinum (Thüm.) Sacc., Syll. Fung. (Abellini) 4: 701. 1886.

Fusarium sclerotium Wollenw., Ber. Deutsch. Bot. Ges. 31: 31. 1913.

Fusarium sclerodermatis var. *lycoperdonis* Picb., Bull. Ecol. Sup. Agron., Brno 13: 27. 1929.

Fusarium scirpi var. *comma* Wollenw., Fus. Autog. Del. 3: no. 922. 1930.

Fusarium scirpi var. *nigrantum* F.T. Benn. (as '*nigrans*'), Ann. Appl. Biol. 19: 26. 1932.

Fusarium scirpi var. *pallens* F.T. Benn., Ann. Appl. Biol. 19: 21. 1932.

Description — See Burgess et al. (1985).

Notes — All synonyms of *F. scirpi* listed above are sensu Wollenweber & Reinking (1935). *Fusarium scirpi* is currently treated as a synonym of *F. acuminatum* in Index Fungorum. Morphologically, *F. scirpi* can be distinguished from *F. acuminatum* by the pigmentation of cultures on PDA (brown with dark brown flecks in *F. scirpi* vs rose to burgundy pigmentation in *F. acuminatum*) and macroconidial septation (6–7-septate in *F. scirpi* vs 3–5-septate in *F. acuminatum*; Booth 1971, Burgess et al. 1985). *Fusarium acuminatum* grouped in the *F. tricinctum* species complex (FTSC; O'Donnell et al. 2013), which formed a distinct lineage distant from the FIESC (Sandoval-Denis et al. 2018a), and the type specimens of these two species showed low similarity (82 %) in *EF-1α* locus. Based on the evidence above, we treat *F. acuminatum* and *F. scirpi* as two distinct species, and resurrect the name *F. scirpi*.

Fusarium sulawense N. Maryani et al., Persoonia 43: 65. 2019

Materials examined. China, Fujian Province, from *Colocasia esculenta*, Aug. 2016, *L. Cai* (LC12177); ibid., from *Ipomoea aquatica*, Aug. 2016, *L. Cai* (LC12175); ibid., from *Ipomoea batatas*, Aug. 2016, *L. Cai* (LC12174); ibid., from *Luffa aegyptiaca*, Aug. 2016, *L. Cai* (LC12173, LC12176); Guangdong Province, Guangzhou, from leaf of *Musa nana*, Aug. 2016, *Y.Z. Diao* (LC12149); ibid., from leaf of *M. nana*, June 2017, *M.M. Wang* (LC12148); Shenzhen, from *Syngonium auritum*, Nov. 2016, *Y.Z. Diao* (LC12178); Guangxi Province, Chongzuo, from fruit of *M. nana*, June 2017, *M.M. Wang* (LC12151, LC12152); Guilin, from stem of *M. nana*, June 2017, *M.M. Wang* (LC12169); Liuzhou, from leaf of *M. nana*, Aug. 2016, *Y.Z. Diao* (LC12153); Nanning, from leaf of *M. nana*, Aug. 2016, *Y.Z. Diao* (LC12170); Hainan Province, from leaf of *Musa paradisiaca*, Dec. 2015, *F.J. Liu* (LC6990, LC7014, LC7019, LC7040); ibid., from *Zea* sp., Apr. 2016, *X.F. Liu* (LC7842); Hubei Province, from *Oryza sativa*, Jan. 2015, *X. Zhou* (LC6928, LC6936); Hunan Province, from *Citrus reticulata*, Jan. 2015, *X. Zhou* (LC6897); Jiangxi Province, Nanchang, from leaf of bamboo, *J.E. Huang* (LC7157, LC7210); Shandong Province, from fruit of *Capsicum* sp., Sept. 2015, *Y.Z. Diao* (LC7919, LC7920, LC7939).

Notes — The isolates of *F. sulawense* clustered in the FIESC 16/17 clade, which were collected from banana in China, Congo and the Kalimantan and Sulawesi islands of Indonesia (O'Donnell et al. 2009, Maryani et al. 2019b). Maryani et al. (2019b) in this volume described it as a novel species. In the present study, two isolates (LC12151, LC12152) of *F. sulawense* were directly isolated from the crown rot of banana fruit, which suggests it might be a new postharvest pathogen of banana.

DISCUSSION

This study was prompted by the confusion of species delineation in the FIESC. By combining molecular phylogeny and morphological characteristics, our assessment clarified some of the phylogenetic relationships within FIESC. Fourteen species were confidently determined in the FIESC in this study, which included five previously known species, i.e., *Fusarium compactum*, *F. equiseti*, *F. lacernatum*, *F. scirpi* and *F. sulawense* (Saccardo 1886, Raillo 1950, Subrahmanyam 1983, Burgess et al. 1985, Maryani et al. 2019b) and nine novel species. The remaining 19 known phylogenetic species can only be resolved and formally named once their morphological features have been determined and documented. The name *F. scirpi* (Burgess et al. 1985) was resurrected in this study based on morphological and phylogenetic data. *Fusarium incarnatum* is not treated in this study, as no type specimen was designated (Saccardo 1886), and no isolate included in this study could be used for typification of this species.

No sexual morphs were observed during the examination of the various isolates studied. Leslie & Summerell (2006) suggested that the sexual morph of *F. equiseti* could be linked to *Gibberella intricans*. However, the taxonomic status of *G. intricans* is uncertain as the type specimen of this species was not designated (Wollenweber 1930). According to the original morphological description, *G. intricans* could easily be distinguished from *F. equiseti* based on the shape of the apical cell and septation of its macroconidia (tapering to whip-like apical cell, 3–12-septate, usually 5–7 in *F. equiseti* vs papillate to hooked apical cell, 3–5-septate in *G. intricans*; Wollenweber 1930, Wollenweber & Reinking 1935). Fresh collections from the original hosts and locality are needed for the epitypification to stabilise the use of the name *G. intricans*.

A number of older names have been considered as synonyms of *F. equiseti* and *F. scirpi* (Wollenweber & Reinking 1935). *Fusarium falcatum* var. *fuscum* and *Fusisporium ossicola* were

excluded in a list of synonyms of *F. equiseti* based on their original morphological descriptions (Berkeley 1875, Sherbakoff 1915). *Fusarium mucronatum* and *Fusoma ossicolum* are currently not recorded and accepted in Index Fungorum or MycoBank, as well as in general literature (Leslie & Summerell 2006). *Fusarium incarnatum* was historically treated as a synonym of *F. semitectum* (Wollenweber & Reinking 1935). However, type specimens of both *F. incarnatum* and *F. semitectum* were not designated (Berkeley 1875, Saccardo 1886). According to the original descriptions, the two species should be considered distinct, and are distinguished from each other by the shape of the macroconidia (fusiform, falcate in *F. incarnatum* vs oblong-clavate in *F. semitectum*).

The polyphasic approach using multi-locus phylogeny, morphological observations and distribution patterns, was found to be effective in classifying species in the FIESC. In our phylogenetic analysis, an updated backbone tree of the FIESC based on ITS, *EF-1α, CAM*, *RPB1* and *RPB2* is provided, which included more plant-inhabiting isolates. The *RPB1* locus was introduced into phylogenetic analyses of the FIESC for the first time. The *RPB2* phylogeny showed better resolution at the species level (Fig. S1) compared to ITS, *EF-1α*, *CAM* and *RPB1*. Multi-locus phylogenetic analyses are necessary in delimitation of the various FIESC species, since no single locus could resolve all known species. All 14 species treated here were separated by high support values (PP ≥ 0.95 and BS ≥ 80; Fig. 1).

Detailed morphological observation forms an important part in the classification of species in the genus *Fusarium*. In the present study, standardised cultural methods according to Gerlach & Nirenberg (1982), Leslie & Summerell (2006) and Sandoval-Denis et al. (2018a) were employed for morphological examinations. Although the FIESC species usually share some overlapping morphological characters, our results revealed that features of the macroconidia are most useful in diagnosis, especially the shape of the apical cell, and conidial size and septation. For example, *F equiseti* was similar to *F. ipomoeae* in the spindle-shaped macroconidia, but they could be differentiated based on the shape of the apical cell and macroconidial septation (tapering to whip-like apical cell, 3–12-septate, usually 5–7-septate in *F. equiseti* vs hooked to tapering apical cell, 3–5-septate in *F. ipomoeae*; Wollenweber & Reinking 1935, Leslie & Summerell 2006). It is also necessary to consider cultural characters on different media when distinguishing species with similar macroconidia. For instance, *F. arcuatisporum* and *F. ipomoeae* are indistinguishable in the shape of their 5-septate macroconidia, but could be distinguished based on cultural characters (undulate margin in *F. arcuatisporum* vs lobate margin in *F. ipomoeae* on PDA, erose margin in *F. arcuatisporum* vs lobate margin in *F. ipomoeae* on SNA, and dense aerial mycelia in *F. arcuatisporum* vs scant aerial mycelia in *F. ipomoeae* on OA).

Several species in the FIESC showed certain habitat preferences. For example, all isolates of *F. citri* and *F. humuli* were isolated from plants, while the *F. scirpi* isolates originated from soil, and *F. hainanense* strains were collected in tropical or subtropical regions (Fig. 1, Table 1). At least 26 phylogenetic species in the FIESC have been recorded from plants worldwide (O'Donnell et al. 2009, 2012), among which eight are described in the present paper (Fig. 1, Table 1). This study mainly focused on the plant-associated FIESC isolates, and also expands our knowledge on the host range of the FIESC species. In this study, six FIESC species are recorded from 17 plant species (17 genera) for the first time (Fig. 1), i.e., *Amygdalus triloba*, *Cedrela* sp., *Colocasia esculenta*, *Hibiscus syriacus*, *Hosta* sp., *Humulus scandens*, *Ligustrun lucidum*, *Liquidambar formosana*, *Luffa aegyptiaca*, *Osmanthus* sp., *Paederia foetida*, *Rosa sempervirens*, *Rhododendron pulchrum*, *Solanum lycopersicum*, *Syngonium auritum*, *Vibumum* sp. and *Vinca major*. *Fusarium sulawense* was obtained from both symptomatic and asymptomatic banana tissues, which supported the hypothesis that endophytes can be latent pathogens (Photita et al. 2001, Romero et al. 2001, Liu et al. 2015).

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Supplementary material

Fig. S1 Fifty percent majority rule consensus tree from a Bayesian analysis based on ITS (a), *EF-1α* (b), *CAM* (c), *RPB1* (d) and *RPB2* (e) shows phylogenetic affinities of species within the FIESC. The Bayesian posterior probabilities (PP > 0.9) and PhyML Bootstrap support values (BS > 70) are displayed at the nodes (PP/ML). The tree was rooted to *F. polyphialidicum* NRRL 13459).