



Fusarium incarnatum-equiseti complex from China

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Key words

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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-1 α*), 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 chlamyospores, 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. chlamyosporum* 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 (Khoá 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, Raillio 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- α | CAM | RPB1 | RPB2 |
|-------------------------|----------------------------|---|-----------------------------------|---------------------|----------|--------------|----------|----------|----------|
| <i>F. arcuatisporum</i> | FIESC 7 | LC11639 | <i>Oryza</i> sp. | Hainan, China | MK280840 | MK289586 | MK289658 | MK289798 | MK289736 |
| | | LC6026 | <i>Nelumbo nucifera</i> leaf | Jiangxi, China | MK280792 | MK289585 | MK289667 | MK289800 | MK289770 |
| | | LC12147 = CGMCC3.19493 (T) | <i>Brassica campestris</i> pollen | Hubei, China | MK280802 | MK289584 | MK289697 | MK289799 | MK289739 |
| | | NRRL 32997 = UTHSC 99-423 | Human toenail | Colorado, America | GQ505713 | GQ505624 | GQ505536 | HM347164 | GQ505802 |
| <i>F. citri</i> | FIESC 29 | LC4879 | <i>Arnydalis triloba</i> | Beijing, China | MK280820 | MK289615 | MK289665 | MK289827 | MK289768 |
| | | LC6896 = CGMCC3.19467 (T) | <i>Citrus reticulata</i> leaf | Hunan, China | MK280803 | MK289617 | MK289668 | MK289828 | MK289771 |
| | | LC7922 | <i>Capsicum</i> sp. | Shandong, China | MK280817 | MK289634 | MK289687 | MK289829 | MK289788 |
| | | LC7937 | <i>Capsicum</i> sp. | Shandong, China | MK280797 | MK289640 | MK289693 | MK289830 | MK289794 |
| <i>F. compactum</i> | | NRRL 25084 = ARSEF 1641 | <i>Adeiphocoris</i> sp. | Austria | JF740883 | JF740715 | - | - | - |
| | | NRRL 52765 = ARSEF 2304 | <i>Heteropsylla cubana</i> | Papua New Guinea | - | JF740839 | - | - | JF741165 |
| | 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 |
| <i>F. equiseti</i> | FIESC 14 | NRRL 36323 = CBS 186.31 (T) | <i>Gossypium</i> sp. | England | GQ505737 | GQ505648 | GQ505560 | - | GQ505826 |
| | | NRRL 20697 = CBS 245.61 | Beet | Chile | GQ505883 | 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 |
| <i>F. guilinese</i> | FIESC 21 | NRRL 36321 = CBS 185.34 | Soil | Netherlands | GQ505736 | GQ505647 | GQ505559 | - | GQ505825 |
| | | NRRL 36466 = CBS 414.86 | <i>Solanum tuberosum</i> | Denmark | GQ505742 | GQ505653 | GQ505565 | - | GQ505831 |
| | | NRRL 43636 = UTHSC 06-170 | Dog | Texas, America | GQ505752 | GQ505663 | GQ505574 | HM347189 | GQ505841 |
| | | LC12160 = CGMCC3.19495 (T) | <i>Musa nana</i> leaf | Guangxi, China | MK280837 | MK289594 | MK289652 | MK289831 | MK289747 |
| <i>F. hainanense</i> | FIESC 26 | NRRL 13335 = FRC R-2138 | Alfalfa | Australia | GQ505679 | GQ505590 | GQ505502 | - | GQ505768 |
| | | NRRL 32865 = FRC R-8480 | Human endocarditis | Brazil | GQ505703 | GQ505614 | GQ505526 | HM347161 | GQ505792 |
| | | LC11638 = CGMCC3.19478 (T) | <i>Oryza</i> sp. stem | Hainan, China | MK280836 | MK289581 | MK289657 | MK289833 | MK289735 |
| | | LC12161 | <i>Musa nana</i> leaf | Guangxi, China | MK280793 | MK289595 | MK289648 | MK289832 | MK289748 |
| <i>F. humuli</i> | FIESC 33 | NRRL 26417 = CBS 544.96 | Leaf litter | Cuba | GQ505687 | GQ505598 | GQ505510 | JX171522 | GQ505776 |
| | | NRRL 28714 = ATCC 74289 | <i>Acacia</i> sp. branch | Costa Rica | GQ505693 | GQ505604 | GQ505516 | - | GQ505782 |
| | | CQ1027 | <i>Ligustrum lucidum</i> leaf | Jiangsu, China | MK280843 | MK289567 | MK289709 | MK289838 | MK289721 |
| | | CQ1032 | <i>Cedrela</i> sp. leaf | Jiangsu, China | MK280844 | MK289568 | MK289710 | MK289839 | MK289722 |
| <i>F. ipomoeae</i> | FIESC 1 | CQ1039 = CGMCC3.19374 (T) | <i>Humulus scandens</i> leaf | Jiangsu, China | MK280845 | MK289570 | MK289712 | MK289840 | MK289724 |
| | | CQ1048 | <i>Viburnum</i> sp. leaf | Jiangsu, China | MK280850 | MK289571 | MK289713 | MK289841 | MK289725 |
| | | CQ1073 | <i>Liquidambar formosana</i> leaf | Jiangsu, China | MK280848 | MK289572 | MK289714 | MK289842 | MK289726 |
| | | CQ1133 | <i>Vinca major</i> leaf | Jiangsu, China | MK280847 | MK289575 | MK289717 | MK289843 | MK289729 |
| | CQ969 | <i>Rosa sempervirens</i> leaf | Jiangsu, China | MK280849 | MK289576 | MK289718 | MK289844 | MK289731 | |
| | CQ970 | <i>Rosa sempervirens</i> leaf | Jiangsu, China | MK280846 | MK289577 | MK289719 | MK289845 | MK289732 | |
| | CQ975 | <i>Paederia foetida</i> leaf | Jiangsu, China | MK280846 | MK289578 | MK289720 | MK289846 | MK289745 | |
| | LC12158 | <i>Musa nana</i> leaf | Guangdong, China | MK280823 | MK289592 | MK289645 | MK289834 | MK289746 | |
| | LC12159 | <i>Musa nana</i> leaf | Guangdong, China | MK280827 | MK289593 | MK289646 | MK289835 | MK289745 | |
| | LC4490 | <i>Osmantthus</i> sp. | Jiangxi, China | MK280826 | MK289614 | MK289664 | MK289836 | MK289767 | |
| | LC7003 | <i>Musa paradisiaca</i> | Hainan, China | MK280833 | MK289623 | MK289674 | MK289837 | MK289777 | |
| | CQ1099 | <i>Rhododendron pulchrum</i> leaf | Jiangsu, China | MK280853 | MK289573 | MK289715 | MK289861 | MK289727 | |
| | CQ1132 | <i>Vinca major</i> leaf | Jiangsu, China | MK280854 | MK289574 | MK289716 | MK289862 | MK289728 | |
| | LC0166 | <i>Solanum lycopersicum</i> fruit | Beijing, China | MK280780 | MK289579 | MK289659 | MK289848 | MK289733 | |
| | LC0455 | <i>Hosta</i> sp. | Beijing, China | MK280819 | MK289580 | MK289660 | MK289849 | MK289734 | |
| | LC12162 | <i>Musa nana</i> leaf | Guangxi, China | MK280795 | MK289596 | MK289655 | MK289847 | MK289749 | |
| | LC12163 | <i>Hibiscus syriacus</i> | Fujian, China | MK280790 | MK289597 | MK289700 | MK289857 | MK289750 | |
| | LC12164 | <i>Hibiscus syriacus</i> | Fujian, China | MK280822 | MK289598 | MK289701 | MK289858 | MK289751 | |
| | LC12165 = CGMCC3.19496 (T) | <i>Ipomoea aquatica</i> leaf | Fujian, China | MK280832 | MK289599 | MK289704 | MK289859 | MK289752 | |
| | LC12166 | <i>Lagenaria siceraria</i> | Fujian, China | MK280791 | MK289600 | MK289706 | MK289860 | MK289753 | |
| | LC5912 | Submerged wood | Jiangxi, China | MK280821 | MK289616 | MK289666 | MK289850 | MK289769 | |
| | LC6926 | <i>Oryza sativa</i> | Hubei, China | MK280799 | MK289619 | MK289670 | MK289851 | MK289773 | |

Table 1 (cont.)

| Species | Phylogenetic species | Strain number and status* | Isolate habitat/host | Location | ITS | EF-1 α | CAM | RPB1 | RPB2 | |
|----------------------------|----------------------------|------------------------------------|------------------------------|-----------------------|------------------|---------------|----------|----------|----------|----------|
| <i>F. ipomoeae</i> (cont.) | | LC7150 | Bamboo | Jiangxi, China | MK280818 | MK289627 | MK289678 | MK289852 | MK289781 | |
| | | LC7923 | <i>Capsicum</i> sp. | Shandong, China | MK280800 | MK289635 | MK289688 | MK289853 | MK289789 | |
| | | LC7925 | <i>Capsicum</i> sp. | Shandong, China | MK280796 | MK289636 | MK289689 | MK289854 | MK289790 | |
| | | LC7936 | <i>Capsicum</i> sp. | Shandong, China | MK280785 | MK289639 | MK289692 | MK289855 | MK289793 | |
| | | LC7940 | <i>Capsicum</i> 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 | |
| | <i>F. irregularis</i> | | 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 | GQ505698 | GQ505607 | GQ505519 | – | GQ505785 |
| | | NRRL 32175 = MDA F10 | Human sputum | Texas, America | GQ505696 | 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 | GQ505530 | – | 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 | | |
| <i>F. lacertarum</i> | | LC7927 | <i>Capsicum</i> sp. | Shandong, China | MK280838 | MK289637 | MK289690 | MK289866 | MK289791 | |
| | | LC7931 | <i>Capsicum</i> sp. | Shandong, China | MK280801 | MK289638 | MK289691 | MK289867 | MK289792 | |
| | | LC7942 | <i>Capsicum</i> sp. | Shandong, China | MK280834 | MK289643 | MK289696 | MK289868 | MK289797 | |
| | | NRRL 20423 = IMI 300797 (T) | Lizard skin | India | GQ505682 | GQ505593 | GQ505505 | JX171467 | GQ505771 | |
| <i>F. luffae</i> | | NRRL 36123 = CBS 102300, BBA 70843 | Unknown | Unknown | GQ505732 | GQ505643 | GQ505555 | – | GQ505821 | |
| | | CQ1038 | <i>Humulus scandens</i> leaf | Jiangsu, China | MK280852 | MK289569 | MK289711 | MK289870 | MK289723 | |
| | | LC12167 = CGMCC3.19497 (T) | <i>Luffa aegyptiaca</i> | Fujian, China | MK280807 | MK289601 | MK289698 | MK289869 | MK289754 | |
| | | NRRL 32522 = Loyola W-14182 | Human diabetic cellulitis | Illinois, America | GQ505701 | GQ505612 | GQ505524 | HM347158 | GQ505790 | |
| <i>F. nanum</i> | | NRRL 31167 | Human sputum | Texas, America | GQ505697 | GQ505608 | GQ505520 | – | GQ505786 | |
| | | LC12168 = CGMCC3.19498 (T) | <i>Musa nana</i> leaf | Guangxi, China | MK280794 | MK289602 | MK289651 | MK289871 | MK289755 | |
| | | LC1384 | <i>Solanum lycopersicum</i> | Saudi Arabia | MK280842 | MK289611 | MK289661 | MK289872 | MK289764 | |
| | | LC1385 | <i>Solanum lycopersicum</i> | Saudi Arabia | MK280781 | MK289612 | MK289662 | MK289873 | MK289765 | |
| | | LC1516 | <i>Solanum lycopersicum</i> | Saudi Arabia | MK280782 | MK289613 | MK289663 | MK289874 | MK289766 | |
| | | NRRL 22244 = H.-K. Chen F64 | <i>Oryza</i> 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 | |
| | | NRRL 13402 = FRC R-6363 | Pine soil | Australia | GQ505681 | GQ505592 | GQ505504 | – | GQ505770 | |
| | | NRRL 26992 = CBS 610.95 | Soil | France | GQ505694 | GQ505605 | GQ505517 | – | GQ505783 | |
| <i>F. scirpi</i> | | NRRL 29134 = CBS 448.84 | Pasture soil | Australia | GQ505743 | GQ505654 | GQ505566 | – | GQ505832 | |
| | | NRRL 36478 = CBS 447.84 | Pasture soil | Australia | GQ505743 | GQ505654 | GQ505566 | – | GQ505832 | |
| <i>F. sulawense</i> | | LC12148 | <i>Musa nana</i> leaf | Guangdong, China | MK280778 | MK289587 | MK289644 | MK289801 | MK289740 | |
| | | LC12149 | <i>Musa nana</i> leaf | Guangdong, China | MK280783 | MK289588 | MK289647 | MK289802 | MK289741 | |
| | | LC12151 | <i>Musa nana</i> fruit | Guangxi, China | MK280825 | MK289589 | MK289649 | MK289803 | MK289742 | |
| | | LC12152 | <i>Musa nana</i> fruit | Guangxi, China | MK280824 | MK289590 | MK289650 | MK289804 | MK289743 | |

Table 1 (cont.)

| Species | Phylogenetic species | Strain number and status* | Isolate habitat/host | Location | ITS | EF-1 α | CAM | RPB1 | RPB2 |
|-----------------------------|------------------------------------|-----------------------------------|------------------------------|------------------|----------|---------------|----------|----------|----------|
| <i>F. solawense</i> (cont.) | | LC12153 | <i>Musa nana</i> leaf | Guangxi, China | MK280779 | MK289591 | MK289654 | MK289806 | MK289744 |
| | | LC12169 | <i>Musa nana</i> stem | Guangxi, China | MK280784 | MK289603 | MK289653 | MK289805 | MK289756 |
| | | LC12170 | <i>Musa nana</i> leaf | Guangxi, China | MK280841 | MK289604 | MK289656 | MK289807 | MK289757 |
| | | LC12173 | <i>Luffa aegyptiaca</i> | Fujian, China | MK280788 | MK289605 | MK289699 | MK289821 | MK289758 |
| | | LC12174 | <i>Ipomoea batatas</i> | Fujian, China | MK280815 | MK289606 | MK289702 | MK289822 | MK289759 |
| | | LC12175 | <i>Ipomoea aquatica</i> | Fujian, China | MK280808 | MK289607 | MK289703 | MK289823 | MK289760 |
| | | LC12176 | <i>Luffa aegyptiaca</i> | Fujian, China | MK280839 | MK289608 | MK289705 | MK289824 | MK289761 |
| | | LC12177 | <i>Colocasia esculenta</i> | Fujian, China | MK280809 | MK289609 | MK289707 | MK289825 | MK289762 |
| | | LC12178 | <i>Syngonium auritum</i> | Guangdong, China | MK280789 | MK289610 | MK289708 | MK289826 | MK289763 |
| | | LC6897 | <i>Citrus reticulata</i> | Hunan, China | MK280810 | MK289618 | MK289669 | MK289808 | MK289772 |
| | | LC6928 | <i>Oryza sativa</i> | Hubei, China | MK280835 | MK289620 | MK289671 | MK289809 | MK289774 |
| | | LC6936 | <i>Oryza sativa</i> | Hubei, China | MK280828 | MK289621 | MK289672 | MK289810 | MK289775 |
| | | LC6990 | <i>Musa paradisiaca</i> leaf | Hainan, China | MK280814 | MK289622 | MK289673 | MK289811 | MK289776 |
| | | LC7014 | <i>Musa paradisiaca</i> leaf | Hainan, China | MK280786 | MK289624 | MK289675 | MK289812 | MK289778 |
| | | LC7019 | <i>Musa paradisiaca</i> leaf | Hainan, China | MK280816 | MK289625 | MK289676 | MK289813 | MK289779 |
| | | LC7040 | <i>Musa paradisiaca</i> 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 | <i>Zea</i> sp. | Hainan, China | MK280813 | MK289631 | MK289684 | MK289817 | MK289785 |
| | LC7919 | <i>Capsicum</i> sp. fruit | Shandong, China | MK280811 | MK289632 | MK289685 | MK289818 | MK289786 | |
| | LC7920 | <i>Capsicum</i> sp. fruit | Shandong, China | MK280805 | MK289633 | MK289686 | MK289819 | MK289787 | |
| | LC7939 | <i>Capsicum</i> sp. fruit | Shandong, China | MK280806 | MK289641 | MK289694 | MK289820 | MK289795 | |
| | NRR1 32864 = FRC R-7245 | Human | Texas, America | GQ505702 | GQ505613 | GQ505525 | HM347160 | GQ505791 | |
| | NRR1 34004 = UTHSC 94-2581 | Human | Texas, America | GQ505717 | GQ505628 | GQ505540 | HM347167 | GQ505806 | |
| | NRR1 34056 = Loyola M54234 | Human bronchial wash | Texas, America | GQ505729 | GQ505640 | GQ505552 | - | GQ505819 | |
| | NRR1 34059 = Loyola S8158 | Human blood | Illinois, America | GQ505730 | GQ505641 | GQ505553 | - | GQ505818 | |
| | NRR1 34070 = Loyola W37591 | Tortoise | Illinois, America | GQ505731 | GQ505642 | GQ505554 | - | GQ505820 | |
| | NRR1 36548 = CBS 190.60 | <i>Musa nana</i> | Congo | GQ505744 | GQ505655 | GQ505567 | - | GQ505833 | |
| FIESC 2 | NRR1 43730 = CDC 2006743605 | Contact lens | Mississippi, America | EF453193 | GQ505669 | GQ505580 | - | GQ505847 | |
| | NRR1 36448 = CBS 384.92 | <i>Gossypium</i> sp. | Mozambique | GQ505740 | GQ505651 | GQ505582 | - | GQ505829 | |
| FIESC 5 | NRR1 25795 = CBS 394.93, BBA 64265 | <i>Phaseolus vulgaris</i> seed | Sudan | GQ505741 | GQ505652 | GQ505564 | - | GQ505830 | |
| | NRR1 32871 = FRC R-9561 | <i>Disphyma crassifolium</i> seed | Germany | GQ505742 | GQ505597 | GQ505509 | - | GQ505775 | |
| | NRR1 34032 = UTHSC 98-2172 | Human abscess | Texas, America | GQ505708 | GQ505619 | GQ505531 | - | GQ505797 | |
| | NRR1 34035 = UTHSC 91-569 | Human abscess | Texas, America | GQ505724 | GQ505635 | GQ505547 | HM347171 | GQ505813 | |
| | NRR1 34037 = UTHSC 02-966 | Human sinus | Colorado, America | GQ505726 | GQ505637 | GQ505549 | - | GQ505815 | |
| | NRR1 45995 = UTHSC 02-966 | Human abscess | Colorado, America | GQ505727 | GQ505638 | GQ505550 | - | GQ505816 | |
| | NRR1 45997 = UTHSC 04-1902 | Human abscess | Colorado, America | GQ505759 | GQ505670 | GQ505581 | - | GQ505848 | |
| FIESC 6 | NRR1 43638 = UTHSC R-3500 | Human sinus | Colorado, America | GQ505761 | GQ505672 | GQ505583 | - | GQ505850 | |
| | NRR1 43694 = CDC 2006743607 | Manatee | Florida, America | GQ505754 | GQ505665 | GQ505576 | - | GQ505843 | |
| | NRR1 45998 = UTHSC 06-2315 | Human eye | Texas, America | GQ505757 | GQ505668 | GQ505579 | HM347193 | GQ505846 | |
| FIESC 8 | NRR1 43496 | Human toe | Texas, America | GQ505762 | GQ505673 | GQ505584 | - | GQ505851 | |
| | NRR1 5537 = ATCC 28805 | Human eye | Pennsylvania, America | GQ505747 | GQ505658 | - | HM347181 | GQ505836 | |
| FIESC 10 | NRR1 3020 = FRC R-6053, 7.12 MRC | <i>Festuca</i> sp. | Missouri, America | GQ505677 | GQ505588 | GQ505500 | - | GQ505766 | |
| | NRR1 3214 = FRC R-6054, 7.13 MRC | Unknown | Missouri, America | GQ505675 | GQ505586 | GQ505498 | - | GQ505764 | |
| FIESC 11 | NRR1 36372 = CBS 235.79 | Unknown | Unknown | GQ505676 | GQ505587 | GQ505499 | - | GQ505765 | |
| FIESC 12 | NRR1 26921 = CBS 731.87 | Air | Antilles, Netherlands | GQ505738 | GQ505649 | GQ505561 | - | GQ505827 | |
| | NRR1 31011 = BBA 69079 | <i>Triticum</i> sp. | Germany | GQ505689 | GQ505600 | GQ505512 | - | GQ505778 | |
| | NRR1 36269 = CBS 162.57 | <i>Thuja</i> sp. | Germany | GQ505695 | GQ505606 | GQ505518 | - | GQ505784 | |
| | NRR1 36392 = CBS 259.54 | <i>Pinus nigra</i> seedling | Croatia | GQ505734 | GQ505645 | GQ505557 | - | GQ505823 | |
| | NRR1 6548 = IMI 112503 | Unknown plant seedling | Germany | GQ505739 | GQ505650 | GQ505562 | - | GQ505828 | |
| FIESC 13 | NRR1 43635 = UTHSC 06-638 | <i>Triticum</i> sp. | Germany | GQ505678 | GQ505589 | GQ505501 | - | GQ505767 | |
| FIESC 19 | NRR1 43639 = UTHSC 04-135 | Horse | Nebraska | GQ505751 | GQ505662 | GQ505573 | HM347188 | GQ505840 | |
| | | Manatee | Florida, America | GQ505755 | GQ505666 | GQ505577 | HM347190 | GQ505844 | |

Table 1 (cont.)

| Species | Phylogenetic species | Strain number and status* | Isolate habitat/host | Location | ITS | EF-1 α | CAM | RPB1 | RPB2 |
|---------------------------|----------------------|------------------------------------|---|----------------------|----------|---------------|----------|----------|----------|
| FIESC 20 | | NRRL 34003 = UTHSC 95-28 | Human sputum | Texas, America | GQ505716 | GQ505627 | GQ505539 | HM347166 | GQ505805 |
| FIESC 22 | | NRRL 36575 = CBS 976.97 | <i>Juriperus chinensis</i> leaf | Hawaii, America | GQ505745 | GQ505656 | GQ505568 | – | GQ505834 |
| FIESC 23 | | NRRL 34002 = UTHSC 95-1545 | Human ethmoid sinus | Texas, America | GQ505715 | GQ505626 | GQ505538 | HM347165 | GQ505804 |
| | | NRRL 13379 = FRC R-5198; BBA 62200 | <i>Oryza sativa</i> | 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 | <i>Spartina rhizomes</i> | Connecticut, America | GQ505746 | GQ505657 | GQ505569 | – | GQ505835 |
| FIESC 27 | | NRRL 20722 = IMI 190455 | <i>Chrysanthemum</i> 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 | <i>Prosopis</i> nr. <i>bicincta</i> on <i>Cynodon</i> | Costa Rica | JF740833 | JF740833 | – | – | JF741159 |
| FIESC 31 | | ITEM11401 | <i>Avena sativa</i> | Canada | – | LN901578 | LN901594 | – | LN901611 |
| | | ITEM13601 | <i>Zea</i> sp. | Netherlands | – | – | – | – | LN901614 |
| FIESC 32 | | CBS 143595 | <i>Ganoderma</i> sp. | Iran | LT970814 | LT970778 | LT970731 | – | LT970750 |
| | | CBS 143596 | <i>Stereum irsutum</i> | 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 |
| <i>F. polyphialiticum</i> | – | 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:

- clarify the phylogenetic and taxonomic relationships of species within the FIESC; and
- 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 mm²) 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 μ L 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 | | |
| <i>EF-1α</i> | 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 | | |
| <i>CAM</i> | 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 | | |
| <i>RPB1</i> | 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 | GTCATYTGDDTGDGCDGGYTCDCC | | |
| <i>RPB2</i> | 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 | | |

* 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).

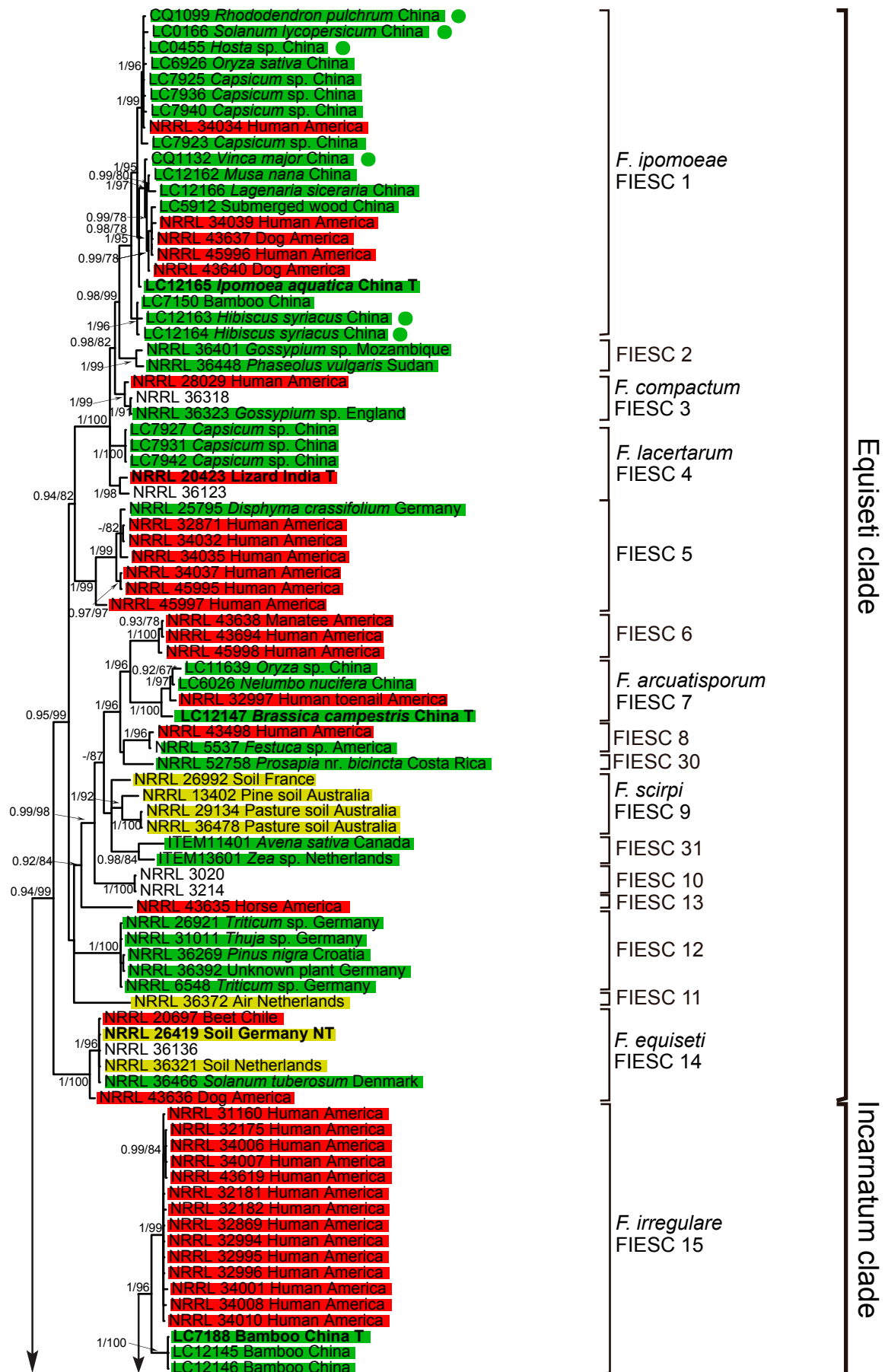


Fig. 1 Fifty percent majority rule consensus tree from a Bayesian analysis based on a five-locus combined dataset (ITS, *EF-1α*, *CAM*, *RPB1* and *RPB2*) showing the phylogenetic relationships of species within the *Fusarium incarnatum-equiseti* species complex (FIESC). The Bayesian posterior probabilities (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.

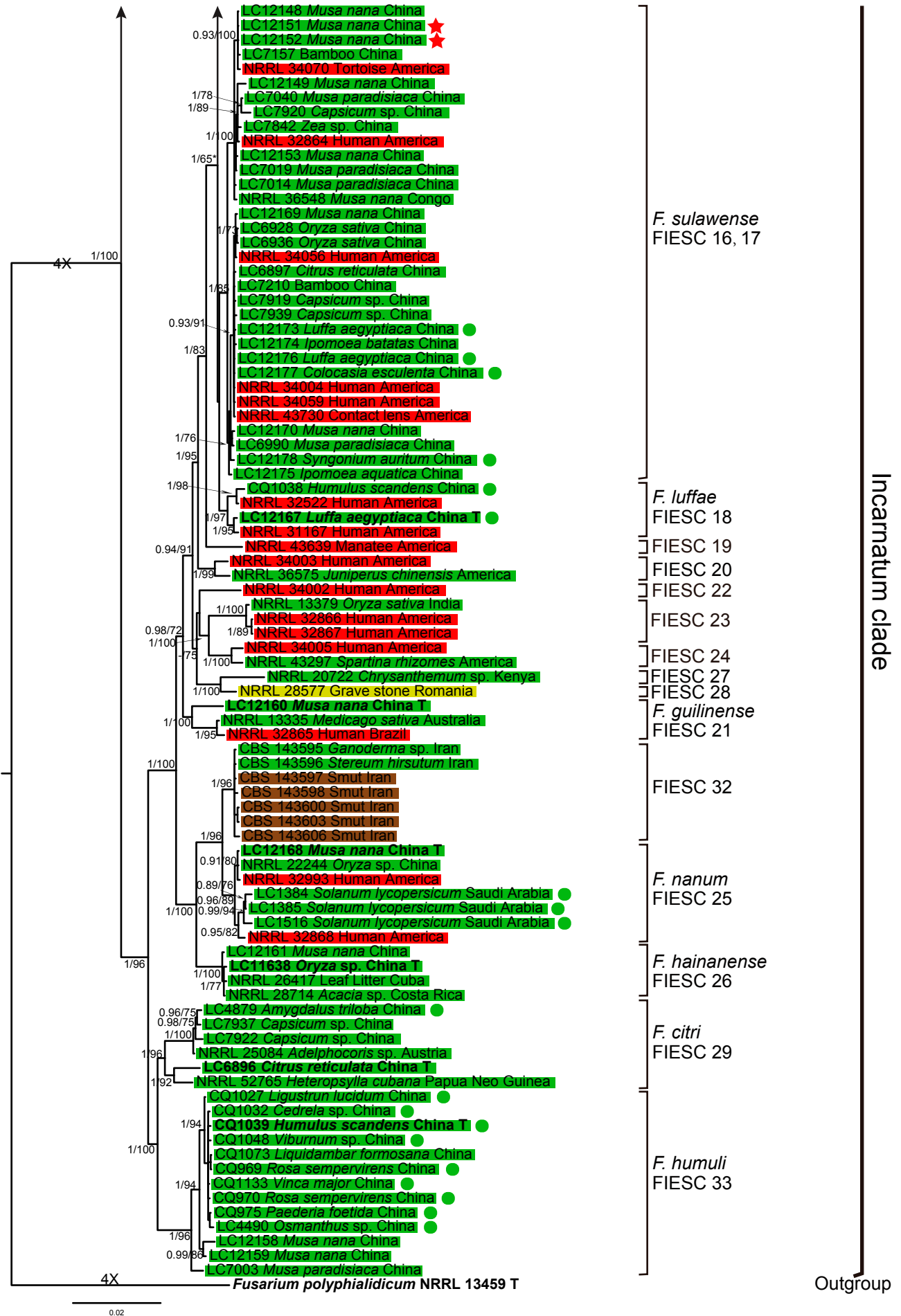


Fig. 1 (cont.)

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 arcuatissporum 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, char-
treuse (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).

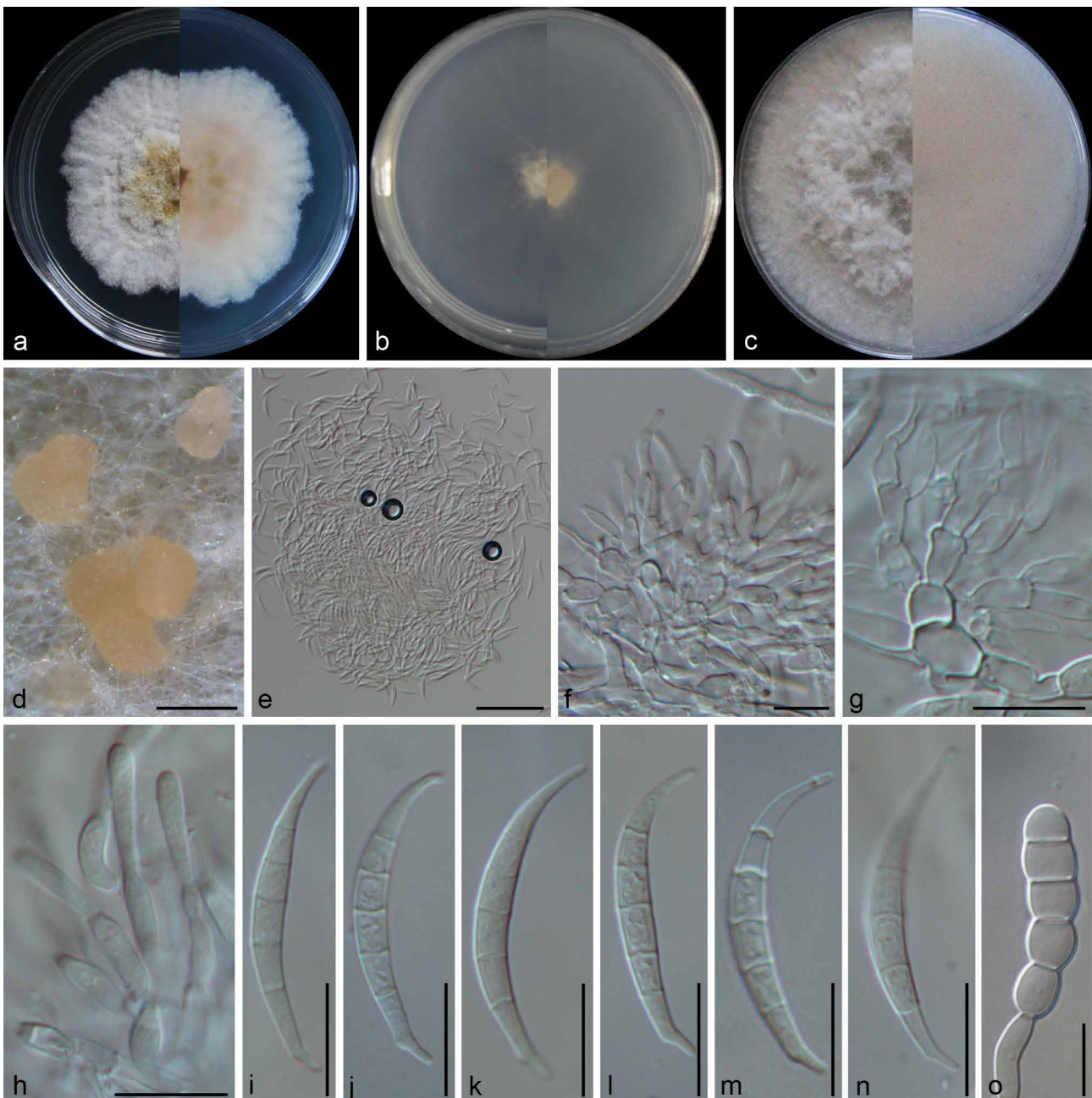


Fig. 2 *Fusarium arcuatissporum* LC12147. a–c. Colonies on PDA, SNA and OA; d–e. sporodochia formed on aerial hyphae on the carnation leaf; f–h. conidiogenous cells form on sporodochia; i–n. macroconidia; o. chlamydospores. — Scale bars: d = 100 µm, e = 50 µm, f–o = 10 µm.

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, $29\text{--}49.5 \times 4\text{--}6 \mu\text{m}$ in *F. arcuatisporum* vs 3–9-septate, usually 6–7-septate, $17\text{--}83 \times 2.5\text{--}6 \mu\text{m}$ in *F. scirpi*) (Wollenweber & Reinking 1935, Leslie & Summerell 2006). Moreover, micro-

conidia 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

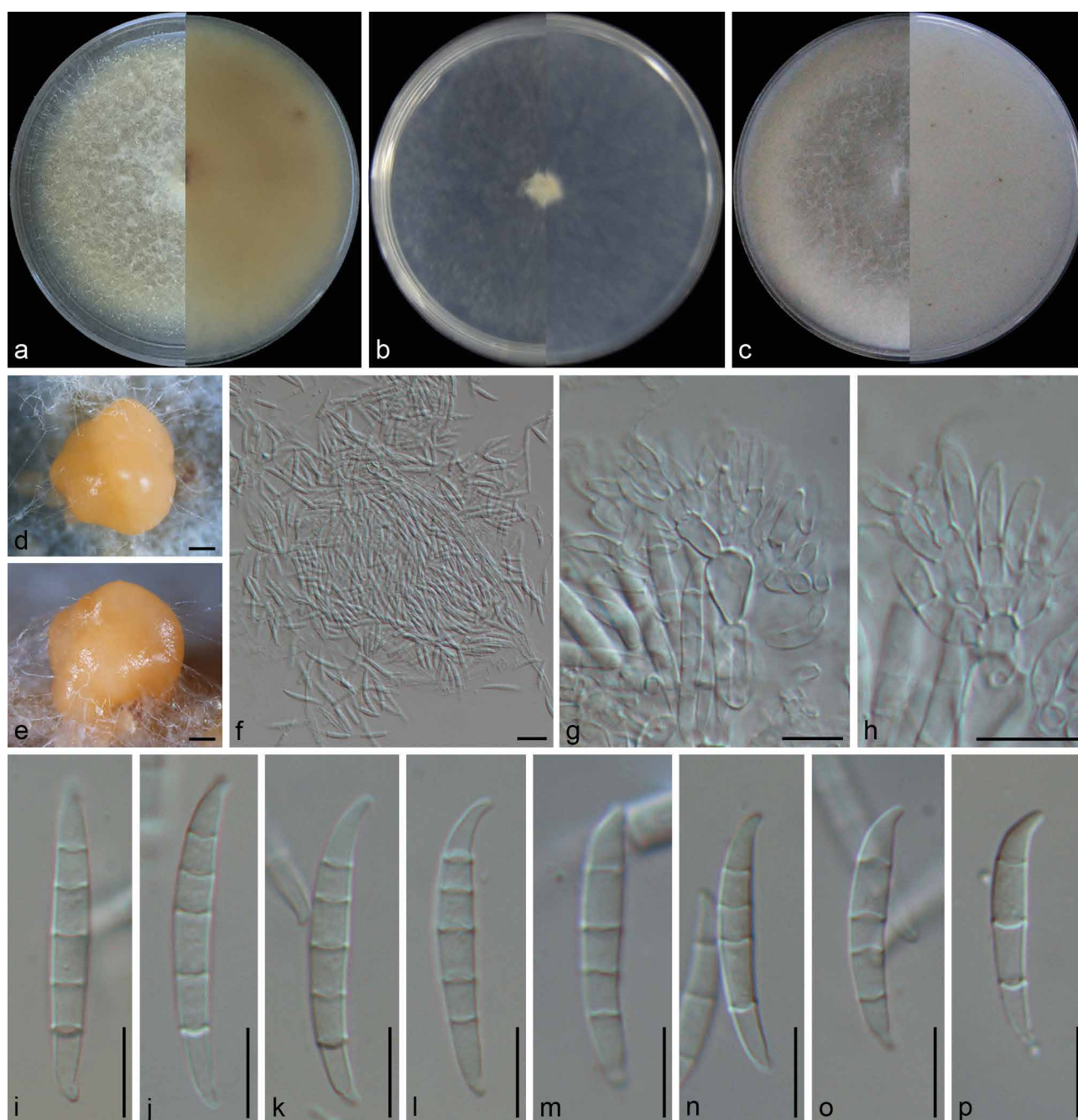


Fig. 3 *Fusarium citri* LC6896. a–c. Colonies on PDA, SNA and OA; d–f. sporodochia formed on the carnation leaf; g–h. conidiogenous cells form on sporodochia; i–p. macroconidia. — Scale bars: d–f = 20 μm , g–p = 10 μm .

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, $7.5\text{--}11.5 \times 2\text{--}4 \mu\text{m}$ (av. \pm SD: $9.4 \pm 0.9 \times 2.9 \pm 0.4 \mu\text{m}$). *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 $25\text{--}31 \times 3.5\text{--}5 \mu\text{m}$ (av. \pm SD: $28.9 \pm 1.4 \times 4 \pm 0.3 \mu\text{m}$); 4-septate macroconidia $30.5\text{--}39 \times 3\text{--}5.5 \mu\text{m}$ (av. \pm SD: $34.7 \pm 1.9 \times 4.2 \pm 0.4 \mu\text{m}$); 5-septate macroconidia $30.5\text{--}40.5 \times 3\text{--}5.5 \mu\text{m}$ (av. \pm SD: $35.3 \pm 2.3 \times 4.2 \pm 0.5 \mu\text{m}$). *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 ($25.5\text{--}40.5 \times 3\text{--}5.5 \mu\text{m}$ in *F. citri* vs $21\text{--}35 \times 2\text{--}3 \mu\text{m}$ in *F. humuli*). All 10 isolates of *F. citri* were obtained from plant hosts, suggesting a potential plant-inhabiting preference.

Fusarium compactum (Wollenw.) Raïllo, *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 Raïllo (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 ossiculum* 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, $11.5\text{--}13 \times 2.5\text{--}3 \mu\text{m}$ (av. \pm SD: $19.8 \pm 3 \times 4.9 \pm 0.2 \mu\text{m}$). *Macroconidia* falcate, slender, straight to curved, smooth to slightly rough, hyaline, apical cell blunt or hooked, basal cell barely to distinctly notched, 3-septate, $20\text{--}39.5 \times 3\text{--}4 \mu\text{m}$ (av. \pm SD: $30 \pm 5.3 \times 3.6 \pm 0.4 \mu\text{m}$); *microconidia* oval, smooth to slightly rough, hyaline, 1-septate, $8\text{--}13.5 \times 3\text{--}4 \mu\text{m}$ (av. \pm SD: $10.4 \pm 1.4 \times 3.4 \pm 0.3 \mu\text{m}$). *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

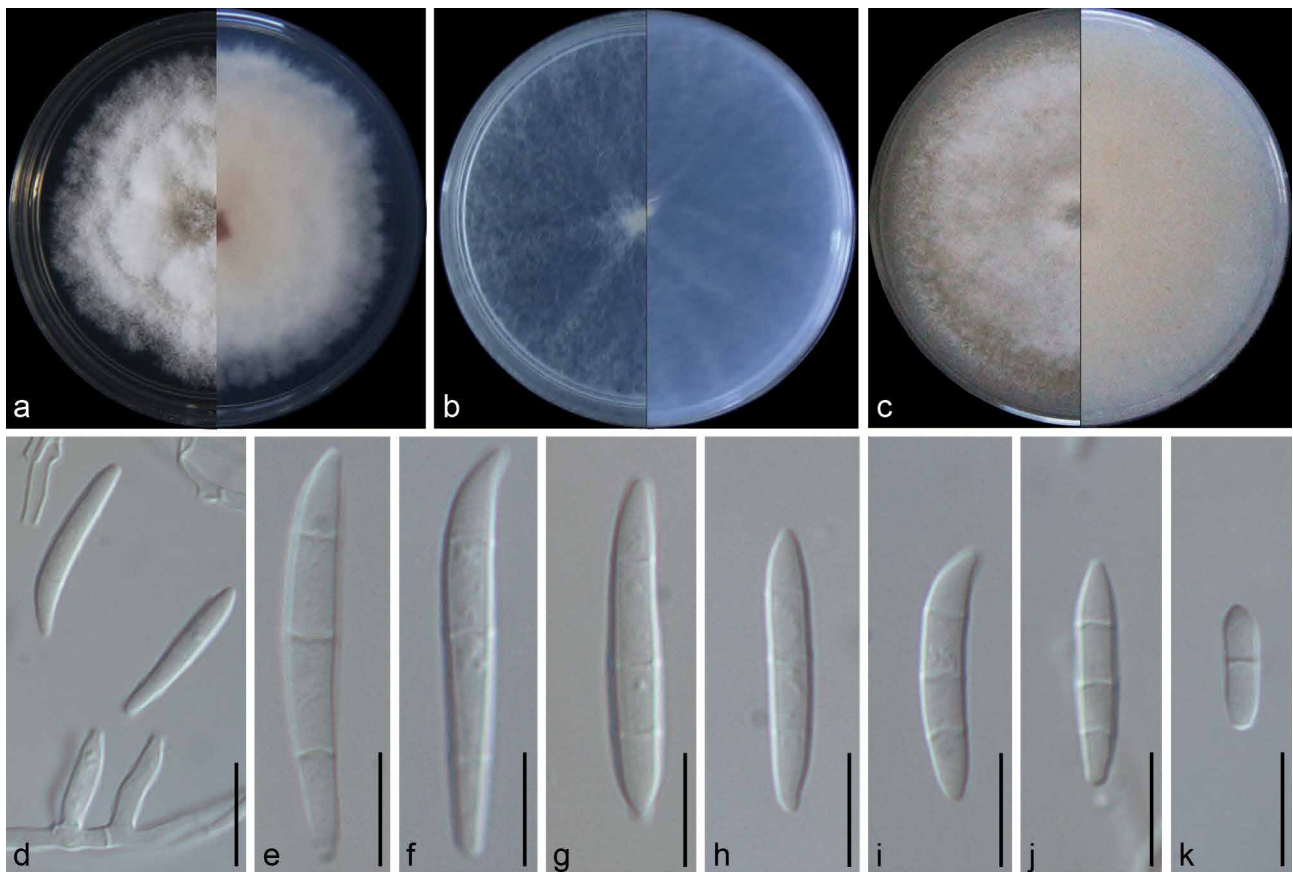


Fig. 4 *Fusarium guilinense* LC12160. a–c. Colonies on PDA, SNA and OA; d. conidiogenous cells form on aerial hyphae; e–k. macroconidia. — Scale bars: d–k = 10 μ m.



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 μ m.

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 \times 2–3 μm (av. \pm SD: 21.5 \pm 0.3 \times 2.4 \pm 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 \times 3–4 μm (av. \pm SD: 20.5 \pm 1.4 \times 3.7 \pm 0.3 μm); 3-septate macroconidia 22–33 \times 2.5–5 μm

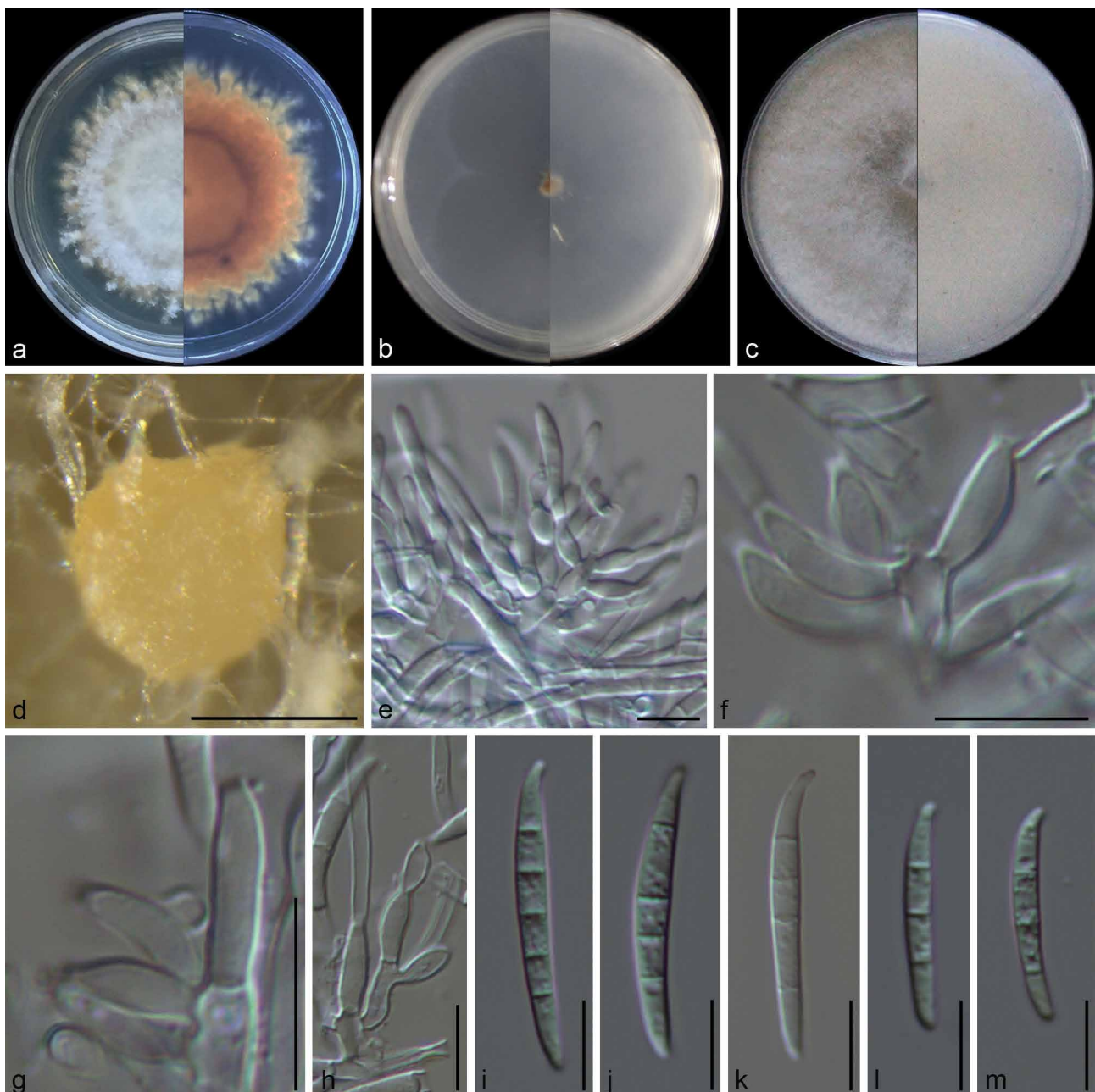


Fig. 6 *Fusarium humuli* CQ1039. a–c. Colonies on PDA, SNA and OA; d–e. sporodochia formed on aerial hyphae; f–h. conidiogenous cells form on sporodochia; i–m. macroconidia. — Scale bars: d = 100 μm , e–m = 10 μm .

(av. \pm SD: $27.5 \pm 3.6 \times 2.7 \pm 0.7 \mu\text{m}$). *Microconidia* not observed. *Chlamydozoospores* 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, $6.3\text{--}11.9 \times 2\text{--}3.4 \mu\text{m}$ (av. \pm SD: $8.7 \pm 2.4 \times 3.1 \pm 0.9 \mu\text{m}$). *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 $21\text{--}23.5 \times 2\text{--}2.5 \mu\text{m}$ (av. \pm SD: $22.5 \pm 0.9 \times 2.3 \pm 0.3 \mu\text{m}$); 4-septate macroconidia $28\text{--}33 \times 2\text{--}3 \mu\text{m}$ (av. \pm SD: $27.5 \pm 1.6 \times 2.7 \pm 0.7 \mu\text{m}$); 5-septate macroconidia $30\text{--}35 \times 2.5\text{--}3 \mu\text{m}$ (av. \pm SD: $32.5 \pm 2.4 \times 2.9 \pm 0.3 \mu\text{m}$). *Microconidia* not observed. *Chlamydozoospores* 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 ($25.5\text{--}40.5 \times 3\text{--}5.5 \mu\text{m}$ in *F. citri* vs $21\text{--}35 \times 2\text{--}3 \mu\text{m}$ 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, $8\text{--}15 \times 2\text{--}4 \mu\text{m}$ (av. \pm SD: $10.9 \pm 1.6 \times 3.5 \pm 0.5 \mu\text{m}$). *Sporodochial macroconidia* with dorsiventral curvature, smooth, hyaline, apical cell hooked to tapering, basal cell foot-shaped, 3–5-septate; 3-septate macroconidia $26.5\text{--}36 \times 3\text{--}3.5 \mu\text{m}$ (av. \pm SD: $32.4 \pm 4.2 \times 3.3 \pm 0.2 \mu\text{m}$); 4-septate macroconidia $36\text{--}38.5 \times 2\text{--}4 \mu\text{m}$ (av. \pm SD: $37.1 \pm 0.9 \times 3.1 \pm 0.6 \mu\text{m}$); 5-septate macroconidia $37.5\text{--}57 \times 2.5\text{--}5 \mu\text{m}$ (av. \pm SD: $44.7 \pm 3.8 \times 3.6 \pm 0.6 \mu\text{m}$). *Microconidia* not observed. *Chlamydozoospores* 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 *Ipomoea 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, $40\text{--}80 \mu\text{m}$ in *F. caudatum* vs 3–5-septate, $26\text{--}57 \mu\text{m}$ 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.

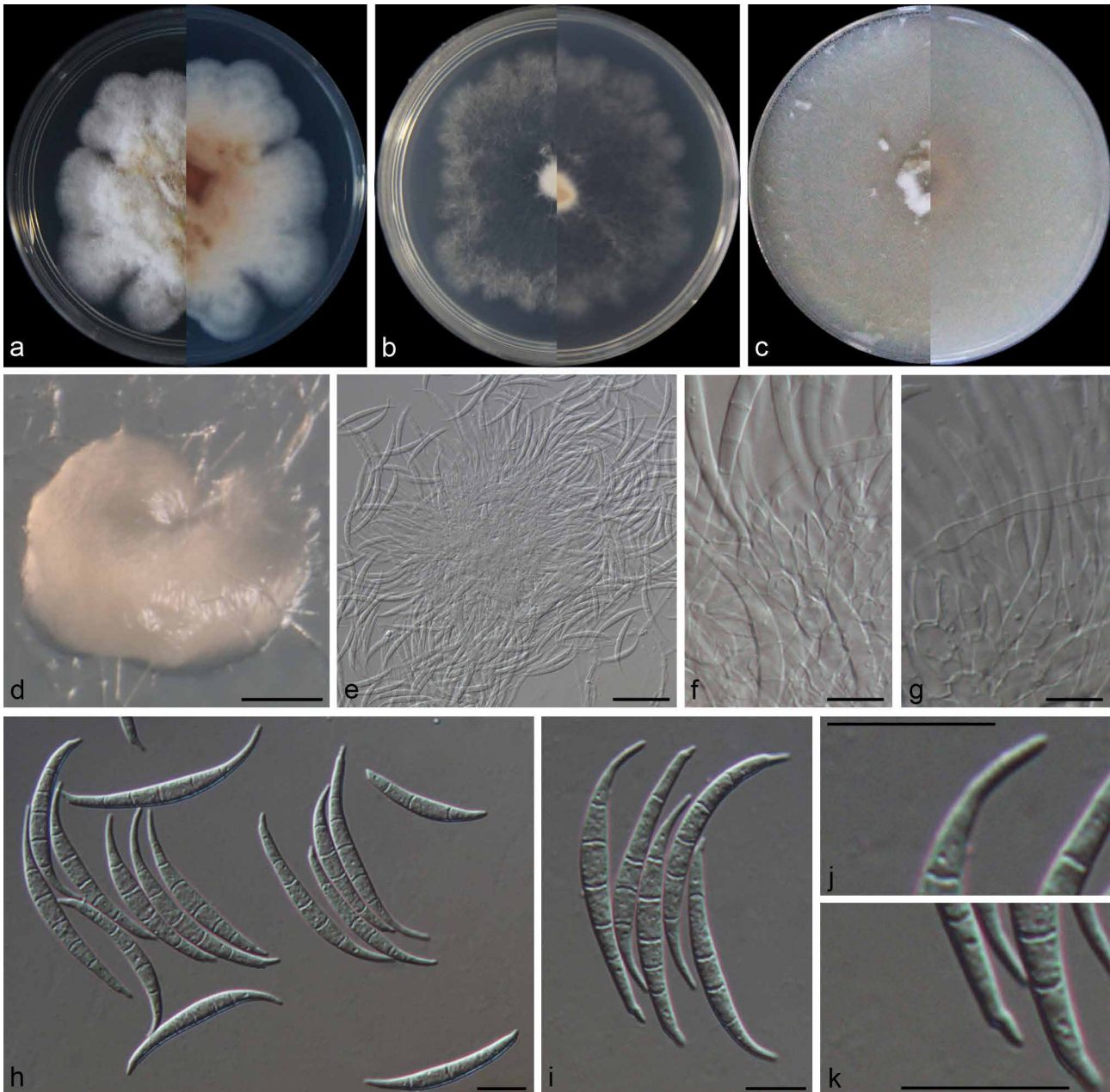


Fig. 7 *Fusarium ipomoeae* LC12165. a–c. Colonies on PDA, SNA and OA; d–e. sporodochia formed on agar near the carnation leaf; f–g. conidiogenous cells form on sporodochia; h–k. macroconidia. — Scale bars: d–e = 50 μ m, f–k = 10 μ m.

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 subcylindri-

cal, smooth and thin-walled, hyaline, 13.5–22.5 \times 2–4 μ m (av. \pm SD: 17.2 \pm 4 \times 3.1 \pm 0.7 μ m). *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 \times 3–5 μ m (av. \pm SD: 25.8 \pm 5.8 \times 3.8 \pm 0.6 μ m). *Microconidia* not observed. *Chlamydozoospores* 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

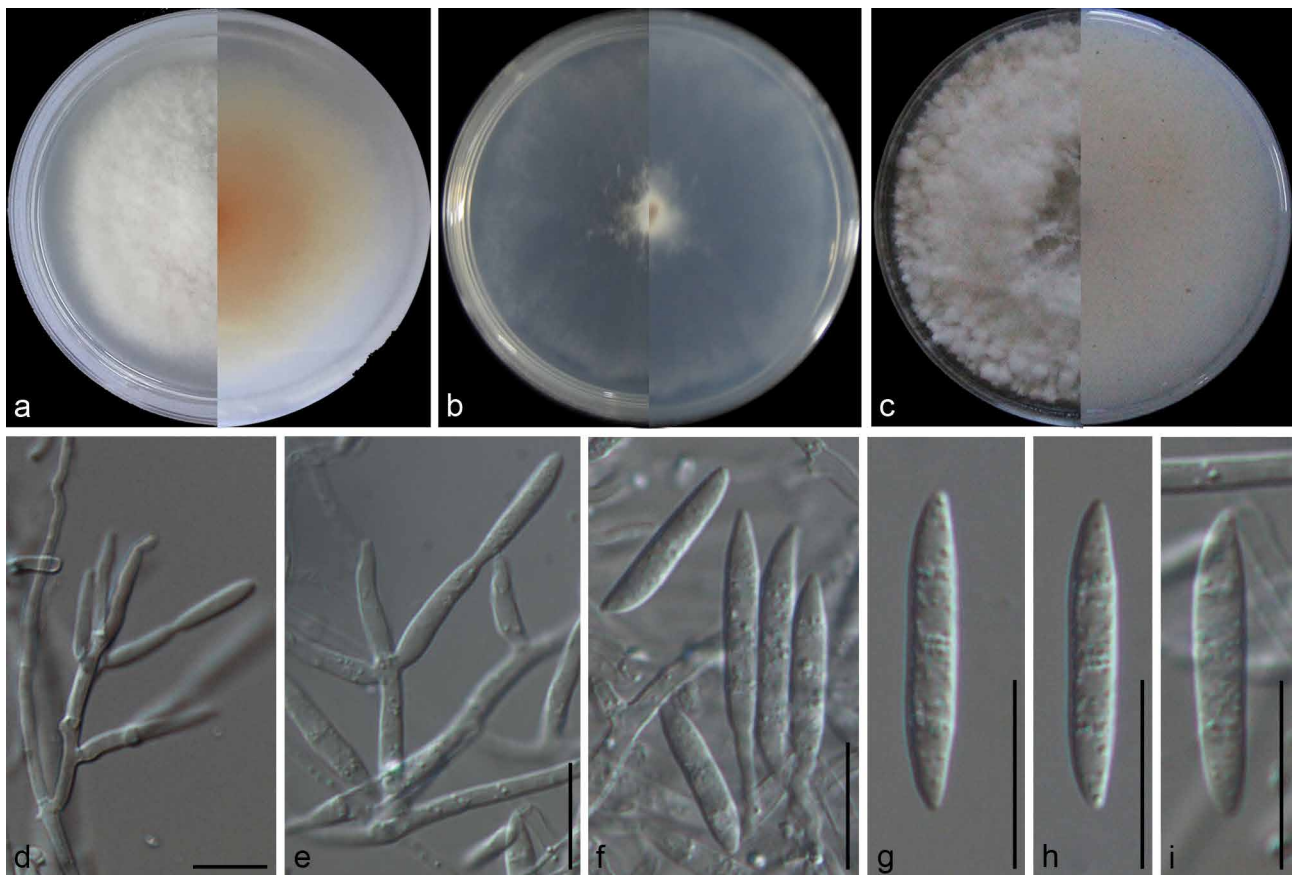


Fig. 8 *Fusarium irregulare* LC7188. a–c. Colonies on PDA, SNA and OA; d–e. conidiophore formed on aerial hyphae; f–i. macroconidia. — Scale bars: d–j = 10 µm.

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).

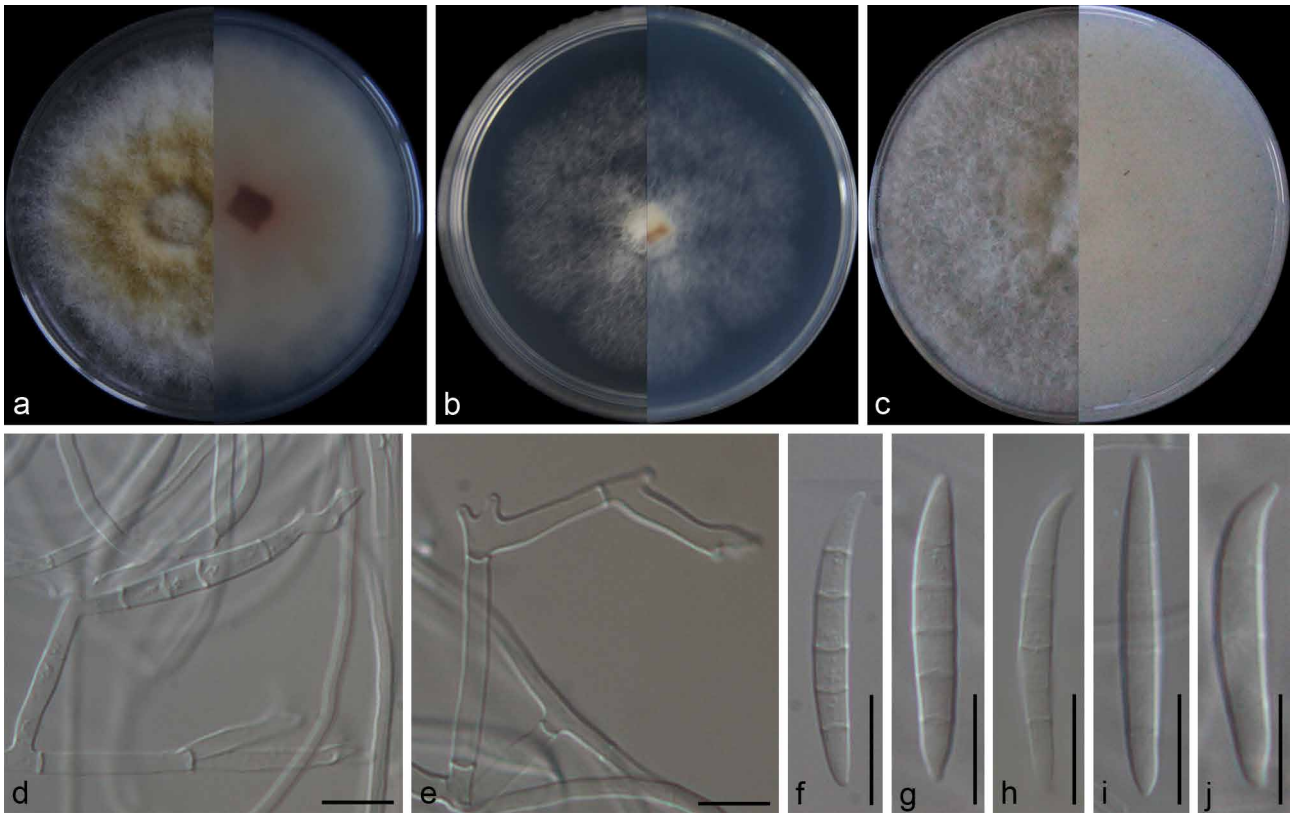


Fig. 9 *Fusarium luffae* LC12167. a–c. Colonies on PDA, SNA and OA; d–e. conidiophores formed on aerial hyphae; f–j. macroconidia. — Scale bars: d–j = 10 μ m.

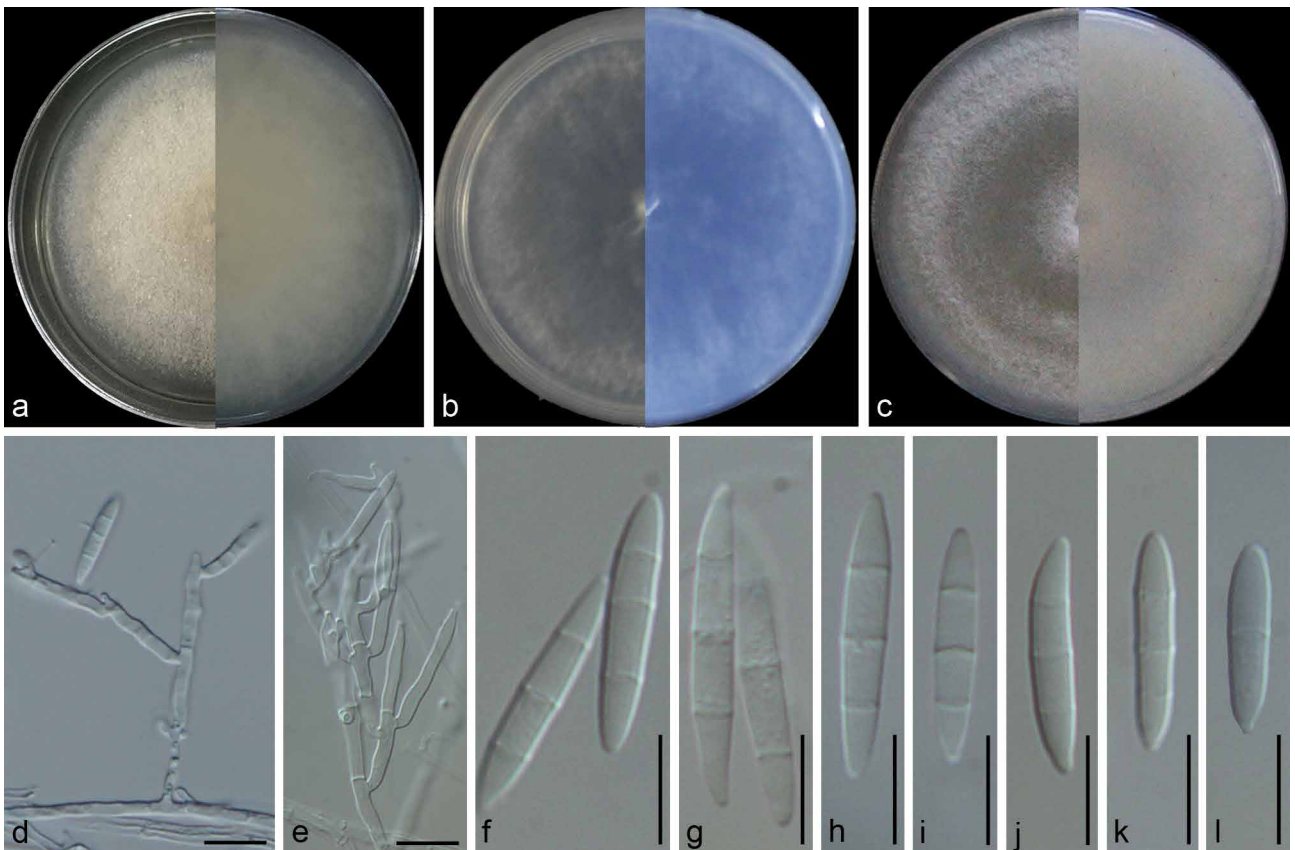


Fig. 10 *Fusarium nanum* LC12168. a–c. Colonies on PDA, SNA and OA; d–e. conidiophores formed on aerial hyphae; f–l. macroconidia. — Scale bars: d–l = 10 μ m.

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). *Microconidia* 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 ossiculum* 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-1 α* , *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-1 α* , *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 \geq 0.95 and BS \geq 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. arcuatissporum* 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. arcuatissporum* vs lobate margin in *F. ipomoeae* on PDA, erose margin in *F. arcuatissporum* vs lobate margin in *F. ipomoeae* on SNA, and dense aerial mycelia in *F. arcuatissporum* 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*, *Ligustrum lucidum*, *Liquidambar formosana*, *Luffa aegyptiaca*, *Osmanthus* sp., *Paederia foetida*, *Rosa sempervirens*, *Rhododendron pulchrum*, *Solanum lyco-*

persicum, *Syngonium auritum*, *Viburnum* 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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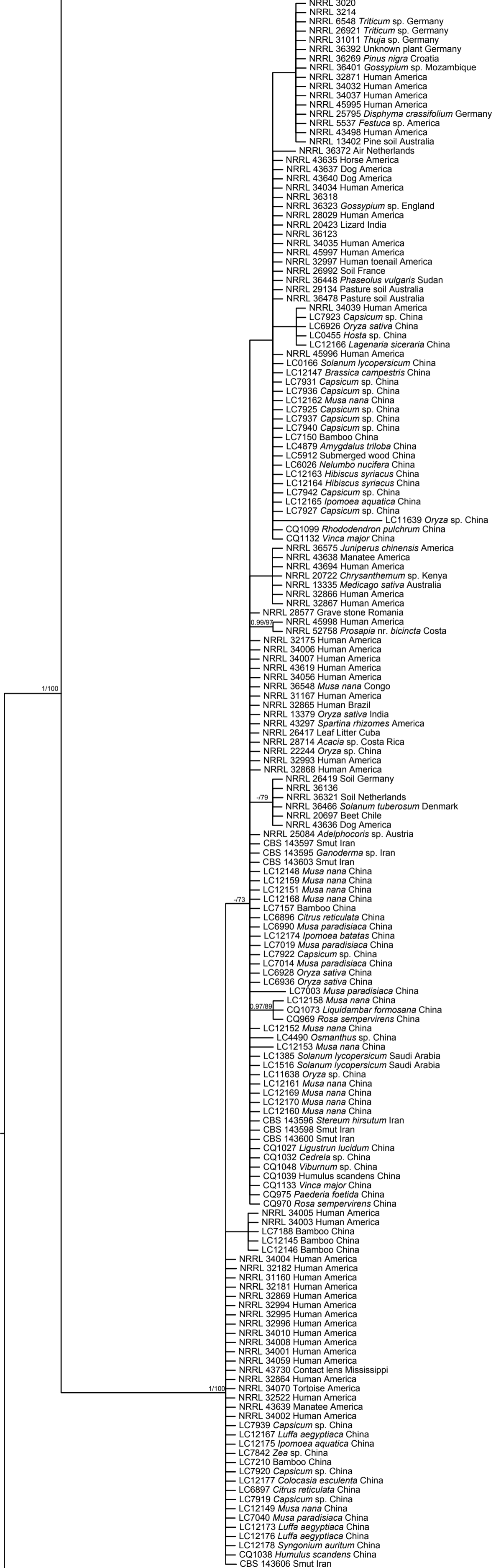
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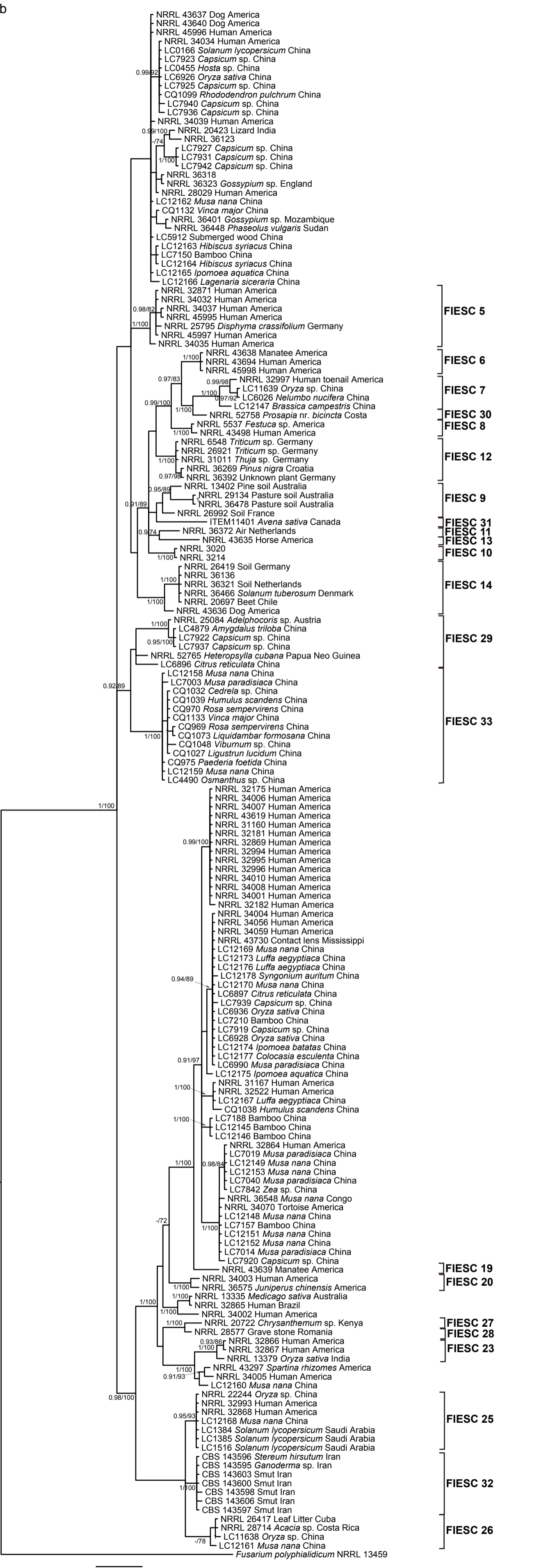
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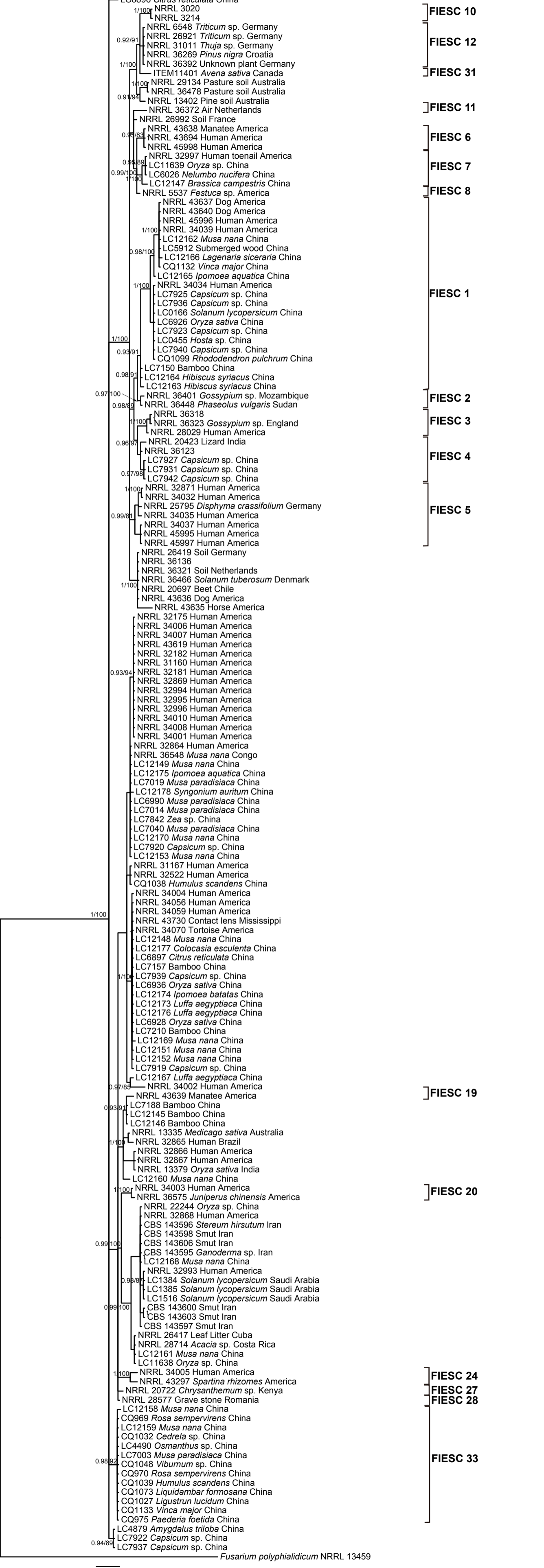
Supplementary material

Fig. S1 Fifty percent majority rule consensus tree from a Bayesian analysis based on ITS (a), *EF-1 α* (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).



Fusarium polyphialidicum NRRL 13459





0.01

Fusarium polyphialidicum NRRL 13459

