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Re-evaluation of *Sympoventuriaceae*

T.P. Wei[1], H. Zhang[1,2], X.Y. Zeng[1], P.W. Crous[3,4,5], Y.L. Jiang[1*]

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Abstract *Sympoventuriaceae* (*Venturiales*, *Dothideomycetes*) comprises genera including saprophytes, endophytes, plant pathogens, as well as important animal or human opportunistic pathogens with diverse ecologies and wide geographical distributions. Although the taxonomy of *Sympoventuriaceae* has been well studied, generic boundaries within the family remain poorly resolved due to the lack of type materials and molecular data. To address this issue and establish a more stable and reliable classification system in *Sympoventuriaceae*, we performed multilocus phylogenetic analyses using sequence data of seven genes (SSU, ITS, LSU, *act1*, *tub2*, *tef1* and *rpb2*) with increased taxon sampling and morphological analysis. The molecular data combined with detailed morphological studies of 143 taxa resolved 22 genera within the family, including one new genus, eight new species, five new combinations and one new name. Finally, we further investigated the evolutionary history of *Sympoventuriaceae* by reconstructing patterns of lifestyle diversification, indicating the ancestral state to be saprophytic, with transitions to endophytic, animal or human opportunistic and plant pathogens.

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INTRODUCTION

Sympoventuriaceae is a large family in *Venturiales* (*Dothideomycetes*, *Ascomycota*) with diverse ecology, wide geographic distribution and rich species diversity (Zhang et al. 2011, Seyedmousavi et al. 2013, Liu et al. 2017, Wijayawardene et al. 2018, Crous et al. 2019a, Shen et al. 2020). Members of this family are usually hyphomycetes with conidia liberated by rhexolytic secession (Seifert et al. 2011, Machouart et al. 2014, Crous et al. 2014, Huanraluek et al. 2019). *Sympoventuriaceae* is mainly known as a ubiquitous environmental saprobic fungus and plant endophytes or pathogens, while a few species have been documented as opportunistic neurotropic pathogens in vertebrate hosts, including humans (Satow et al. 2008, Seyedmousavi et al. 2014, Kidd et al. 2016, Zhang et al. 2018, Samerpitak et al. 2019, Benavent 2021, Murata et al. 2022). They are also known for their thermophilic properties, such as living in hot springs (Revankar & Sutton 2010, Hao et al. 2013, Samerpitak et al. 2014, 2015b, Wang et al. 2018, Crous et al. 2020).

Sympoventuriaceae was introduced by Zhang et al. (2011) with *Sympoventuria* (type genus), *Veronaeopsis* and fusicladium-like species included. The generic organization of sequestrate taxa within the *Sympoventuriaceae* has long been a subject of debate, due to a high level of morphological plasticity, and the lack of molecular data (Machouart et al. 2014, Samerpitak et al. 2016). *Sympoventuria* was first described for a venturia-like ascomycete, typified by *S. capensis*, a species found on decaying leaves of *Eucalyptus*, which was characterised by its saprobic lifestyle, pseudoparaphyses, and hyaline, symmetrical ascospores and subcylindrical asci (Crous et al. 2007a, b). *Veronaeopsis* was introduced as a monotypic genus for *V. simplex*, which was previously separated from *Veronaea* based on its shorter conidiophores, geniculate rachis and prominent conidiogenous loci (Papendorf 1969, Arzanlou et al. 2007). Morphologically, *Sympoventuria* is allied to *Venturia* (Sivanesan 1977, Zhang et al. 2011, Zhang et al. 2016), although their asexual morphs are quite distinct. For instance, *Fusicladium* (asexual morph of *Venturia*) was established by Bonorden (1851) to accommodate *F. virescens*, a well-known pathogen of pears. *Fusicladium* is characterised by sympodial conidiogenesis, differentiated conidiophores, and melanized conidia with dark basal scars. However, the taxonomy of this genus has continued to be controversial (Baldacci & Ciferri 1937, Schubert et al. 2003, Beck et al. 2005, Koukol 2010). Shen et al. (2020) resolved *Fusicladium* as asexual morph of *Venturia*, but also introduced several additional fusicladium-like genera, namely *Fuscohilum*, *Neofusicladium*, *Parafusicladium* and *Pinaceicola*.

Since its introduction, several genera have either been included or excluded from *Sympoventuriaceae*, and many mycologists commented that there might be more unrecognized genera within the family (Machouart et al. 2014, Samerpitak et al. 2016). *Scolecobasidium* (= *Ochroconis*) and *Verruconis* are very similar genera that have sympodial conidiogenous cells and T- or Y-shaped to cylindrical or clavate conidia (Abbott 1927, De Hoog & Von Arx 1973). Due to an unusual combination of morphological and ecological characters, their systematic position has historically been controversial. Samerpitak et al. (2014) distinguished these genera based on their ecological and physiological traits and morphological differences. They

[1] Department of Plant Pathology, College of Agriculture, Guizhou University, Guiyang, 550025, Guizhou Province, China; corresponding author e-mail: yljchsd@163.com.
[2] Guizhou Academy of Testing and Analysis, Guiyang, 550014, Guizhou Province, China.
[3] Westerdijk Fungal Biodiversity Institute, P.O. Box 85167, 3508 AD Utrecht, The Netherlands.
[4] Microbiology, Department of Biology, Faculty of Science, Utrecht University, Padualaan 8, 3584 CT Utrecht, The Netherlands.
[5] Wageningen University and Research Centre (WUR), Laboratory of Phytopathology, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands.

accommodated mesophilic species with smooth-walled to verruculose conidia in *Scolecobasidium* (as *Ochroconis*), and retained the thermophilic taxa with verrucose to coarsely ornamented conidia in *Verruconis*. Nevertheless, morphological and ecological delimitation of *Scolecobasidium* and *Verruconis* is problematic and remains obscure (Samerpitak et al. 2016, Qiao et al. 2019). *Acroconidiellina* was introduced by Ellis (1971) to accommodate *A. arecae*, *A. chloridis*, *A. loudetiae* (type species) and *A. urtiagae*. Hernández-Restrepo et al. (2016) further pointed out that *Acroconidiellina* is allied to the *Scolecobasidium*/*Ochroconis* complex, and belonged to *Sympoventuriaceae* (Li et al. 2016, Wijayawardene et al. 2020). Furthermore, although *Acroconidiellina* currently contains four species, the taxonomic placement of only *A. arecae* has thus far been confirmed based on phylogenetic studies. The monotypic genus *Mycosisymbrium* was proposed by Carris (1994), re-described by Pratibha & Prabhugaonkar (2016), initially regarded as *incertae sedis* in the *Pezizomycotina*, and later placed in *Sympoventuriaceae*. Following these studies, three interesting genera, *Echinocatena*, *Matsushimaea* and *Yunnanomyces* were analysed phylogenetically suggesting a close relationship to *Sympoventuriaceae*, each of which formed a monophyletic clade with other genera in this family (Crous et al. 2018a, b, Tibpromma et al. 2018). *Pseudosigmoidea* (typified by *P. cranei*) was introduced based on species of *Sigmoidea* with enteroblastic conidia and phialidic conidiogenesis (Ando & Nakamura 2000), and subsequent studies showed that it also resided in *Sympoventuriaceae* (Diene et al. 2013, Crous et al. 2019a). Hernández-Restrepo et al. (2020) reassessed the taxonomic placement of *Melnikomyces* to accommodate an increasing number of emerging species, and placed it in *Sympoventuriaceae*, together with other genera producing septate conidia from denticulate conidiogenous cells (Crous et al. 2014, Wei et al. 2020).

The classification of *Sympoventuriaceae* includes a wide range of taxa based on morphological characters, although these are chiefly asexual genera (Zhang et al. 2011, Machouart et al. 2014). However, some genera (e.g., *Clavatispora*, *Neocoleroa*) of *Sympoventuriaceae* were established only based on their sexual morphology, and very few links between sexual and asexual morphs have been confirmed. *Sympoventuria capensis* was introduced with both a sexual and asexual morph (Crous et al. 2007a, Machouart et al. 2014). Subsequently, Boonmee et al. (2014) introduced *Clavatispora* based on the sexual morph *C. thailandica*. Its unique ascospores and bitunicate asci resemble *Pleosporales* species but differ from most other taxa in *Venturiales* (Seifert et al. 2011, Hyde et al. 2013, 2020). In addition, the phylogenetic analysis of conserved genes (nuSSU, nuLSU, mtSSU and *rpb2*) indicated that *Verruconis* is distinct from *Scolecobasidium*, while several related sexual morphs were also included in the *Sympoventuriaceae* (Machouart et al. 2014). Another sexual genus, *Neocoleroa* (typified by *N. sibirica*), is characterised by lobed to dichotomously branched, blunt-tipped setae on superficial pseudothecia (Petrak 1934, Johnston & Park 2016). Morphologically, *Neocoleroa* is most comparable to *Wentiomyces* (Koorders 1907), and they have had a tangled taxonomic history (Barr 1997, Kirk et al. 2008). It is noteworthy, except for a few species of *Clavatispora*, *Neocoleroa*, *Scolecobasidium*, *Sympoventuria* and *Verruconis*, that the sexual morphs of most species of the *Sympoventuriaceae* are unknown. Moreover, the asexual and sexual morphs of *Sympoventuriaceae* often develop separately, or only one morph is formed, making it difficult to confirm links between morphs of the same species.

In summary, *Sympoventuriaceae* has been extensively reviewed in recent years in efforts to clarify the phylogeny and taxonomic relationships of its species and allied fungi, and has resulted in a modern redefinition of the family, which provides a solid foundation to facilitate future DNA phylogenetic studies (Tibpromma et al. 2018, Crous et al. 2019a, Shen et al. 2020). In spite of this, however, many questions remain unresolved about the phylogenetic relationships of some poorly documented taxa, especially genera and species for which molecular data are not yet available. This has justified an urgent need to reconsider the species boundaries for *Sympoventuriaceae* based on a robust family-wide phylogenetic backbone and framework. Furthermore, *Sympoventuriaceae* includes approximately 164 species, is a morphologically and ecologically diverse fungal group with different lifestyles and modes of nutrition (MycoBank, April 2022). In order to adapt to changing environmental conditions, their ecological habitat varies from saprobic, animal or human opportunistic

Table 1 Primers and PCR conditions.

Genes	Primers	Sequences/PCR conditions	References
ITS	ITS5 (Fw)	5′-GGAAGTAAAAGTCGTAACAAGG-3′	White et al. (1990)
	ITS4 (Rw)	5′-TCCTCCGCTTATTGATATGC-3′	White et al. (1990)
		95 °C 5 min, (95 °C 35 s, 56 °C 30 s, 72 °C 1 min) 35 cycles, 72 °C 4 min	
LSU	LR0R (Fw)	5′-ACCCGCTGAACTTAAGC-3′	Vilgalys & Hester (1990)
	LR5 (Rw)	5′-TCCTGAGGGAAACTTCG-3′	Vilgalys & Hester (1990)
		95 °C 5 min, (95 °C 45 s, 56 °C 40 s, 72 °C 2 min) 35 cycles, 72 °C 10 min	
SSU	NS1 (Fw)	5′-GTAGTCATATGCTTGTCTC-3′	White et al. (1990)
	NS24 (Rw)	5′-AAACCTTGTTACGACTTTTA-3′	Gargas & Taylor (1992)
		95 °C 5 min, (95 °C 45 s, 56 °C 40 s, 72 °C 2 min) 35 cycles, 72 °C 10 min	
act1	512 (Fw)	5′-ATGTGCAAGGCCGGTTTCGC-3′	Carbone & Kohn (1999)
	783 (Rw)	5′-TACGAGTCCTTCTGGCCCAT-3′	Carbone & Kohn (1999)
		95 °C 5 min, (96 °C 45 s, 56 °C 30 s, 72 °C 1 min) 35 cycles, 72 °C 5 min	
tub2	Bt2a (Fw)	5-GGTAACCAAATCGGTGCTGCTTTC-3	Glass & Donaldson (1995)
	Bt2b (Rw)	5′-ACCCTCAGTGTAGTGACCCTTGGC-3′	Glass & Donaldson (1995)
		95 °C 5 min, (95 °C 35 s, 56 °C 50 s, 72 °C 2 min) 35 cycles, 72 °C 7 min	
tef1	728 (Fw)	5′-CATCGAGAAGTTCGAGAAGG-3′	Carbone & Kohn (1999)
	986 (Rw)	5′-TACTTGAAGGAACCCTTAC-3′	Carbone & Kohn (1999)
	983 (Fw)	5′-GCYCCYGGHCAYCGTGAYTTYAT-3′	Rehner & Buckley (2005)
	2218 (Fw)	5′-ATGACACCRACRGCRACRGTYTG-3′	Rehner & Buckley (2005)
		95 °C 5 min, (96 °C 45 s, 56 °C 30 s, 72 °C 45 s) 35 cycles, 72 °C 5 min	
rpb2	5 (Fw)	5′-GAYGAYMGWGATCAYTTYGG-3′	Liu et al. (1999)
	7CR (Rw)	5′-CCCATRGCTTGYTTRCCCAT-3′	Liu et al. (1999)
		95 °C 5 min, (96 °C 45 s, 56 °C 30 s, 72 °C 2 min) 35 cycles, 72 °C 5 min	

Table 2 Strains used in the phylogenetic analysis of *Sympoventuriaceae* and GenBank accession numbers.

Species	Strain[1]	Host and substrate	Locality	GenBank accession numbers[2]				
				ITS	LSU	*tub2*	*tef1*	*rpb2*
Acroconidiellina arecae	NFCCI 3696	On little patches on the leaves of *Areca Catechu*	India	KX306747	KX306776	–	–	–
Bellamyces quercus	CBS 46217*	*Lecanora chlarotera* on *Quercus trunks*	UK	MK810901	MK810788	–	MK888726	MK887796
Clavatispora thailandiaca	MFLUCC 100107	On dead stems of herbaceous plants	Thailand	MH065721	KF770458	–	KF770459	–
Echinocatena arthrinioides	CBS 144202	*Acacia crassicarpa*, leaves	Malaysia	MH107890	MH107937	–	–	–
Fuscohilum rhodensis	CBS 121641*	*Ceratonia siliqua*, branches	Greece	MK810909	MK810796	MK926471	MK888733	MK887802
Fu. siciliana	CBS 105.85*	*Chamaerops humilis*	Italy	MK810910	MK810797	MK926472	MK888734	MN091924
Guizhoumyces aciculaea	GUCC 18195*	Isolated from soil	China	**MZ503724**	**MZ503757**	**MZ546903**	**MZ546870**	**MZ546866**
	GUCC 18152	From leaf litter	China	**MZ503723**	**MZ503756**	**MZ546902**	**MZ546869**	**MZ546865**
Helicopsis olivaceum	CBS 728.83	*Dicksonia antarctica*, dead petiole	Australia	MH861681	MH873393	–	–	–
Matsushimaea fasciculata	CBS 167.97*	On dead leaf of *Cinnamomum japonicum*	Japan	LT962397	LT962402	–	–	–
	GUCC 18239	Isolated from soil	China	**MZ503725**	**MZ503758**	**MZ546904**	**MZ546871**	**MZ546867**
Ma. monilioides	CBS 143867*	Garden soil	Spain	LT883468	LT883469	–	–	–
Melnikomyces longisporum	HUGP 18226*	From forest litter	China	MT731290	MT731291	MT739515	MT739516	–
Me. thailandicus	CBS 145767*	Isolated from soil	Thailand	MN794374	MN794351	–	–	–
Me. vietnamensis	CBS 136209*	On dry leaves of broadleaved tree	Vietnam	KJ869156	KJ869213	–	–	–
Mycosisymbrium cirrhosum	MTCC12435	On dead leaves of *Vaccinium macrocarpon*	United States	KR259883	KR259884	–	–	KR349124
	GUCC 1837	Isolated from decaying *Camellia sinensis* leaf litter	China	**MZ503722**	**MZ503755**	**MZ546901**	**MZ546868**	**MZ546864**
Neocoleroa cameroonensis	CBS 129041*	*Crematogaster* sp. (ant) carton on Barteria nigritana	Cameroon	MK810902	MK810789	MN078219	MK888727	MK887797
Nc. metrosideri	ICMP 21139*	On living leaves of *Metrosideros excelsa*	New Zealand	KU131678	KU131677	–	–	–
Neofusicladium eucalypti	CBS 128216*	*Eucalyptus regnans*, leaf litter	Australia	MK810903	MK810790	MK926468	MK888728	MK887798
Nf. eucalypticola	CBS 141301*	*Eucalyptus robusta*, leaf litter	France	MK810904	MK810791	–	MK888729	MK887799
	CBS 143427	*Eucalyptus dunnii*, leaves	Australia	MK810905	MK810792	–	–	–
Nf. regnans	CBS 143411*	*Eucalyptus regnans*, leaves	Australia	MG386066	MG386119	MG386169	–	–
	CBS 144605	On leaves of *Eucalyptus pauciflora* (*Myrtaceae*)	Australia	MK442628	MK442563	MK442748	MK442722	–
Parafusicladium amoenum	CBS 254.95*	*Eucalyptus* sp., fallen leaves	Cuba	MK810906	MK810793	MK926469	MK888730	–
Pa. intermedium	CBS 110746*	*Eucalyptus* sp., leaf litter	Madagascar	MK810907	MK810794	MK926470	MK888731	MK887800
Pa. paraamoenum	CBS 141322*	*Eucalyptus regnans*, leaf litter	Australia	MK810908	MK810795	–	MK888732	MK887801
Pinaceicola cordae	CBS 126959*	*Pinus sylvestris*, litter needles	Czech Republic	MK810911	MK810798	MK926473	MK888735	–
	CBS 675.82	*Pinus sylvestris*, litter needles	Netherlands	MK810912	MK810799	MK926474	MK888736	–
	CBS 143494	*Pinus sylvestris*, litter needles	Germany	MK810913	MK810800	MK926475	MK888737	–
Pi. pini	CBS 463.82*	*Pinus sylvestris*, litter needles	Netherlands	MK810915	MK810802	MK926477	MK888739	MK887804
	CBS 462.82	*Pinus* sp., litter needles	Netherlands	MK810914	MK810801	MK926476	MK888738	MK887803
Pseudosigmoidea alnicola	CBS 145034*	Leaf litter of *Alnus glutinosa* (*Betulaceae*)	Germany	MK442620	MK442556	–	–	–
Ps. excentrica	CBS 469.95*	*Lauraceae*, leaf litter	Cuba	HQ667543	KF282669	MK926478	KF155975	–
Ps. ibarakiensis	NBRC 107891*	Natural forest soil	Japan	LC146758	LC146759	–	–	–
Scolecobasidium anellii	CBS 284.64*	Stalactite	Italy	FR832477	KF156138	KF156184	KF155995	KF282684
Sc. anomala	CBS 131816*	Lascaux Cave	France	HE575201	KF156137	KF156194	KF155986	HE575205
Sc. blechni	CBS 146055*	Leaves of *Blechnum capense* (*Blechnaceae*)	South Africa	MN562134	MN567641	MN556843	MN556826	–
Sc. constricta	CBS 211.53*	Soil	Canada: Ontario	HQ667519	KF156148	KF156187	KF156005	KF282686
Sc. crassihumicola	CBS 120700	Soil	Papua New Guinea	KJ867429	KJ867430	KJ867433	KJ867428	–
Sc. gamsii	CBS 239.78*	*Caryota plumosa*, leaf	Sri Lanka	KF156019	KF156150	KF156190	KF155982	–
Sc. icarus	CBS 536.69*	Forest soil	Canada: Ontario	HQ667524	KF156132	KF156174	KF156009	KF282700
Sc. lascauxensis	CBS 131815*	Black stain on cave sediment	France	FR832474	KF156136	KF156183	KF155994	FR832481
Sc. longiphorum	CBS 435.76*	In excrement of *Insecta*, and *Quercus*	Japan	KF156038	KF156135	KF156182	KF155978	–
Sc. musicola	CBS 144441*	On leaves of *Musa* sp. (*Musaceae*)	Malaysia	MH327824	MH327860	MH327898	MH327887	MH327876
Sc. phaeophora	CBS 206.96*	Leaf in coastal rain forest	Papua New Guinea	KP798631	KP798634	KT272062	KT272098	KF282692
Sc. tshawytschae	CBS 100438*	On young *Oncorhynchus tshawytscha*	USA: California	HQ667562	KF156126	KF156180	KF155990	KF282697
Sc. verrucosa	CBS 383.81*	From soil	India: Kerala	KF156015	KF156129	KF156185	KT272099	–
Sterila eucalypti	CBS 144019*	*Eucalyptus* sp.	Portugal	MK810918	MK810805	–	MK888742	MK887807
	CPC 14942	*Eucalyptus* sp.	Portugal	MK810916	MK810803	–	MK888740	MK887805
	CPC 14943	*Eucalyptus* sp.	Portugal	MK810917	MK810804	–	MK888741	MK887806
Sympoventuria capensis	CBS 120136*	On leaf litter of *Eucalyptus* sp. (*Myrtaceae*)	South Africa	MK810921	MK810808	MK926481	MK888745	MK887810
	CPC 12839	On leaf litter of *Eucalyptus* sp. (*Myrtaceae*)	South Africa	MK810922	MK810809	MK926482	MK888746	MK887811
	CPC 12840	On leaf litter of *Eucalyptus* sp. (*Myrtaceae*)	South Africa	MK810923	MK810810	MK926483	MK888747	MK887812

Table 2 (cont.)

Species	Strain[1]	Host and substrate	Locality	GenBank accession numbers[2]				
				ITS	LSU	*tub2*	*tef1*	*rpb2*
Sy. melaleucae	CBS 143407*	*Melaleuca* sp., leaves	Australia	MG386059	MG386112	MG386168	–	–
Troposporella fumosa	CBS 351.94	On the old bark of *Populus tremula* (*Salicaceae*)	Finland	MK810924	MH874121	–	–	–
Tr. monilipes	MUCL 19867	On decayed wood of *Quercus* (*Fagaceae*)	United States	DQ351723	AY856871	–	–	–
Veronaeopsis simplex	CBS 588.66*	*Acacia karroo*, leaf litter	South Africa	EU041820	EU041877	–	–	MN091925
Verruconis gallopava	CBS 437.64*	*Meleagris gallopavo*, brain abscess	United States	HQ667553	KF156112	KF156203	KF155968	KF282689
Ve. mangrovei	NFCCI-4390*	On decaying wood of *Excoecaria agallocha*	India	MN782361	MN241144	MN848140	–	–
Ve. panacis	CBS 142802*	From the root of *Panax notoginseng*	China	MF536882	MF536880	MF536883	MF536881	–
Ve. pseudotricladiata	YMF1.04915*	Leaves of a broad-leaf species in a stream	China	MK244396	MK248270	MK253013	MK248273	–
Ve. terricola	CBS 131795*	Isolated from soil	China	MK810925	MK810811	–	–	KC337072
Ve. verruculosa	CBS 119775*	Grassland soil	India	KF156014	KF156106	KF156193	KF155974	–
Yunnanomyces pandanicola	MFLUCC 17-2260*	On decaying leaves of *Pandanus amaryllifolius*	China	MH388369	MH376743	–	MH388403	MH412736
Yu. phoenicis	MFLUCC 19-0254*	On fallen rachides and leaves of *Phoenix paludosa*	Thailand	–	MK976738	–	MK986486	MK986484
	MFLUCC 19-0253	On fallen rachides and leaves of *Phoenix paludosa*	Thailand	**–**	MK976737	**–**	MK986485	MK986483
Tyrannosorus lichenicola	CBS 144018*	*Letharia* sp.	USA	MK810953	MK810838	MK926509	MK888775	MK887840
Venturia saliciperda	CBS 480.61*	*Salix cordata*	Switzerland	MK811007	MK810891	MK926558	MK888825	MK887886

[1] CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CPC: Culture collection of Pedro Crous, housed at Westerdijk Fungal Biodiversity Institute; CGMCC: Chinese General Microbiological Culture Collection Center, Beijing, China; GUCC: Culture Collection of the Department of Plant Pathology, Agriculture College, Guizhou University, China; HGUP: Herbarium of the Department of Plant Pathology, Agricultural College, Guizhou University, China; ICMP: International Collection of Micro-organisms from Plants, Landcare Research, Private Bag 92170, Auckland, New Zealand; IRAN: Fungal Culture Collections of the Iranian Research Institute of Plant Protection; MFLU (CC): Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; MUCL: Universite Catholique de Louvain, Louvain-la-Neuve, Belgium. MTCC: Institute of Microbial Technology, Chandigarh, India; NBRC: Biological Resource Center; NFCCI: National Fungal Culture Collection of India, Pune, India.

[2] ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial large subunit (28S) nrRNA gene; SSU: partial small subunit (18S) nrRNA gene; *act1*: actin; *tub2*: partial β-tubulin gene; *tef1*: partial translation elongation factor 1-alpha gene; *rpb2*: partial DNA-directed RNA polymerase II second largest subunit gene. Accession numbers of sequences generated in this study are in **bold**; – indicates unavailable sequences or unknown collection data.

* Ex-holotype or ex-type strains.

and plant pathogens to extremophilic species (thermophilic fungi) (Samerpitak et al. 2019, Benavent 2021, Murata et al. 2022). Apparently, these fungi have evolved different lifestyles to exploit their environment, suggesting that adaptive radiations within *Sympoventuriaceae* was most likely driven by the ecological diversity (Martin et al. 2016, Haridas et al. 2020). Thus, to know more about the evolutionary importance of this feature, a more detailed study on the co-evolutionary history of this fungal group and its association with the environment is necessary, to elucidate the origin of this family and understand the evolutionary patterns of its lifestyles.

In this study, seven DNA barcodes (SSU, ITS, LSU, *act1*, *tub2*, *tef1* and *rpb2*) were sequenced for 33 strains representing *Guizhoumyces* (two isolates), *Matsushimaea* (one isolate), *Mycosisymbrium* (one isolate), *Scolecobasidium* (27 isolates) and *Verruconis* (two isolates). In addition, a multi-locus phylogenetic analysis was performed including 143 taxa of *Sympoventuriaceae*, and ancestral character states of *Sympoventuriaceae* were reconstructed. Our specific goals were as follows:

i determine the taxonomic position of newly collected strains based on morphological and molecular evidence;
ii provide a revised phylogram for *Sympoventuriaceae*;
iii clarify the phylogenetic relationship between *Scolecobasidium* and *Verruconis* and other similar genera; and
iv to reconstruct the ancestral state and clarify the life strategies during the evolutionary history of *Sympoventuriaceae*.

MATERIALS AND METHODS

Fungal materials and isolation

The soil, plant and forest litter were collected from China. Each sample or specimen was separately stored in a zip-lock bag or envelope before returning to the laboratory for isolation. Strains were isolated by dilution plate and single spore isolation methods, and subcultured on 2 % potato dextrose agar (PDA) (Crous et al. 2019b). In the present study, 33 strains from 18 species of *Scolecobasidium* (13 species) and the closely related genera *Guizhoumyces* (one species), *Matsushimaea* (one species), *Mycosisymbrium* (one species) and *Verruconis* (two species) were collected. The samples include five of the 22 recognised genera in *Sympoventuriaceae* plus one genus newly described here. The holotype specimens were deposited in the Herbarium of the Department of Plant Pathology, Agricultural College, Guizhou University (HGUP). The ex-type cultures are conserved in the Culture Collection of the Department of Plant Pathology, Agriculture College, Guizhou University, China (GUCC) and the China General Microbiological Culture Collection Center (CGMCC).

DNA extraction, amplification and sequencing

Genomic DNA was extracted after 7 d from fresh mycelial cultures grown on PDA. Approximately 50 mg mycelium was scraped off the surface of the medium and transferred to a 1.5 mL microcentrifuge tube. The DNA was extracted using the BIOMIGA Fungus Genomic DNA Extraction Kit GD2416 (Biomiga, USA) following the manufacturer's instructions. The partial nucleotide and protein coding genes were subjected to PCR amplification and sequencing of internal transcribed spacer regions and the intervening 5.8S rRNA gene (ITS) of the rDNA operon, 28S rRNA gene (LSU), 18S ribosomal RNA (SSU), actin gene (*act1*), translation elongation factor 1-alpha (*tef1*), RNA polymerase II second largest subunit (*rpb2*) and β-tubulin (*tub2*). For primers and conditions see Table 1. The PCR products were purified and sequenced by Sangon Biotech, and both directions were sequenced to ensure accuracy. The newly generated sequences in this study were deposited in GenBank, the alignments in

Table 3 Strains used in the phylogenetic analysis of *Scolecobasidium* and *Verruconis* and GenBank accession numbers.

Species	Strain[1]	Host and substrate	Locality	GenBank accession numbers[2]					
				SSU	ITS	LSU	*act1*	*tub2*	*tef1*
S. ailanthi	MFLUCC 17-0923*	On fallen pod of *Ailanthus* sp.	Thailand	MK347838	MK347730	MK347947	MK412893	MK412883	–
	MFLU 18-2110	On fallen pod of *Ailanthus* sp.	Thailand	MK347839	MK347731	MK347948	MK412892	MK412881	–
S. anellii	CBS 284.64*	Stalactite	Italy	KF156070	FR832477	KF156138	KF155912	KF156184	KF155995
S. anomalum	CBS 131816*	Lascaux Cave	France	KF156065	HE575201	KF156137	KF155935	KF156194	KF155986
S. aquaticum	CBS 140316*	Silicone	Germany	KX668260	KX668258	KX668259	–	–	–
S. bacilliforme	CBS 100442*	On stainless steel biofilm in drinking water	Germany	KP798638	KP798632	KP798635	KT272051	KT272059	KT272070
S. blechni	CBS 146055*	Leaves of *Blechnum capense*	South Africa	–	MN562134	MN567641	–	MN556843	MN556826
S. camellicola	GUCC 18242*	On decaying *Camellia sinensis* leaf litter	China	**MZ503654**	**MZ503728**	**MZ503761**	**MZ546837**	**MZ546907**	**MZ546874**
	GUCC 18243	On decaying *Camellia sinensis* leaf litter	China	**MZ503655**	**MZ503729**	**MZ503762**	**MZ546838**	**MZ546908**	**MZ546875**
	GUCC 18244	Isolated from forest litter	China	**MZ503656**	**MZ503730**	**MZ503763**	**MZ546839**	**MZ546909**	**MZ546876**
S. capsici	CBS 142096*	Leaf of *Capsicum annuum*	Thailand	–	KY173427	KY173518	–	–	–
S. coiledmyces	GUCC 18245*	Isolated from lawn soil	China	**MZ503657**	**MZ503731**	**MZ503764**	**MZ546840**	**MZ546910**	**MZ546877**
S. constrictum	CBS 211.53*	Soil	Canada: Ontario	KF156073	HQ667519	KF156148	KF155941	KF156187	KF156005
	CBS 131913	Human, cutaneous mycosis	Thailand	KF156071	KF156025	KF156146	KF155940	KF156176	KF156006
	GUCC 18255	Isolated from dead branches	China	**MZ503667**	**MZ503741**	**MZ503774**	**MZ546850**	**MZ546920**	**MZ546887**
	GUCC 18256	Isolated from forest litter	China	**MZ503668**	**MZ503742**	**MZ503775**	**MZ546851**	**MZ546921**	**MZ546888**
	GUCC 18257	Isolated from soil	China	**MZ503669**	**MZ503743**	**MZ503776**	**MZ546852**	**MZ546922**	**MZ546889**
	GUCC 18258	Isolated from lawn soil	China	**MZ503670**	**MZ503744**	**MZ503777**	**MZ546853**	**MZ546923**	**MZ546890**
S. cordanae	CBS 475.80*	*Mauritia minor*, leaf litter	Colombia	KF156058	KF156022	KF156122	HQ916976	KF156197	KF155981
	CBS 412.51	Not available	United States	KF156056	HQ667540	KF156123	KF155907	KF156200	KF155980
S. crassihumicola	CBS 120700	Soil	Papua New Guinea	KJ867431	KJ867429	KJ867430	KJ867427	KJ867433	KJ867428
S. dracaenae	CBS 141323*	Leaf spots of *Dracaena reflexa*	USA	–	KX228283	KX228334	–	–	KX228377
S. echinulatum	GUCC 18247*	Isolated from soil	China	**MZ503659**	**MZ503733**	**MZ503766**	**MZ546842**	**MZ546912**	**MZ546879**
	GUCC 18248	Isolated from soil	China	**MZ503660**	**MZ503734**	**MZ503767**	**MZ546843**	**MZ546913**	**MZ546880**
S. ellipsoideum	CBS 131796*	Soil	China	–	MN077367	–	–	–	–
	GUCC 18264	Isolated from soil	China	**MZ503676**	**MZ503750**	**MZ503783**	**MZ546859**	**MZ546929**	**MZ546896**
	GUCC 18265	Isolated from submerged wood	China	**MZ503677**	**MZ503751**	**MZ503784**	**MZ546860**	**MZ546930**	**MZ546897**
	GUCC 18266	Isolated from forest litter	China	**MZ503678**	**MZ503752**	**MZ503785**	**MZ546861**	**MZ546931**	**MZ546898**
S. ferulica	IRAN3232C*	Root of *Ferula ovina*	Iran	–	MF186874	MH400207	–	–	–
S. gamsii	CBS 239.78*	*Caryota plumosa*, leaf	Sri Lanka	KF156088	KF156019	KF156150	KF155936	KF156190	KF155982
S. globale	CBS 119644*	Indoor sample, house	Germany	KF961108	KF961086	KF961097	KF956086	KF961065	KF961075
	CBS 135924	Bathroom; black biofilm, sink drain	Germany	KF961107	KF961092	KF961104	KF956092	KF961070	KF961079
	GUCC 18249	From forest humus	China	**MZ503661**	**MZ503735**	**MZ503768**	**MZ546844**	**MZ546914**	**MZ546881**
	GUCC 18250	From soil	China	**MZ503662**	**MZ503736**	**MZ503769**	**MZ546845**	**MZ546915**	**MZ546882**
S. guangxiensis	SS23*	Soil and sugarcane root	China	MK929277	MK934570	MK956169	–	–	–
	X22	Soil and sugarcane root	China	MK961269	MK961215	MK961247	–	–	–
S. helicteris	NFCCI 4310*	Living leaves of *Helicteris isora*	India	–	MK014833	–	–	MK321318	–
S. humicola	CBS 116655*	Peat soil	Canada: Ontario	KF156068	HQ667521	KF156124	KF155904	KF156195	KF155984
S. icarus	CBS 536.69*	Forest soil	Canada: Ontario	KF156084	HQ667524	KF156132	KF155944	KF156174	KF156009
	CBS 423.64	Rhizosphere	Netherlands	KF156085	HQ667523	KF156131	KF155943	KF156173	KF156008
S. lascauxense	CBS 131815*	Black stain on cave sediment	France	KF156069	FR832474	KF156136	KF155911	KF156183	KF155994
S. leishanicola	HGUP 1808*	Soil	China	MK377071	MK377301	MK377073	–	–	–
	GUCC 18259	Isolated from soil	China	**MZ503671**	**MZ503745**	**MZ503778**	**MZ546854**	**MZ546924**	**MZ546891**
S. longiphorum	CBS 435.76*	In excrement of *Insecta*, and *Quercus*	Japan	KF156060	KF156038	KF156135	KF155908	KF156182	KF155978
S. macrozamiae	CBS 137971*	*Macrozamia*, leaf litter	Australia	–	KJ869123	KJ869180	–	–	–
	CBS 102491	On leaf litter of *Macrozamia*	Australia	KF156092	KF156021	KF156152	KF155938	KF156191	KF155983
S. minimum	CBS 510.71*	*Gossypium arboreum*, rhizosphere	Nigeria	KF156087	HQ667522	KF156134	KF155945	KF156172	KF156007
	CBS 119792	Soil	India	KF156086	KF156027	KF156133	KF155946	KF156175	KT272073
	GUCC 18260	From forest humus	China	**MZ503672**	**MZ503746**	**MZ503779**	**MZ546855**	**MZ546925**	**MZ546892**
S. mirabilis	CBS 413.51*	Breathing regulator for diver	Netherlands	KF156076	HQ667536	KF156140	KF155957	KF156164	KF156001
S. musae	CBS 729.95*	Regulator of diver	Netherlands	KF156082	KF156029	KF156144	KF155948	KF156171	KF155999
S. musicola	CBS 144441*	On leaves of *Musa* sp. (*Musaceae*)	Malaysia	–	MH327824	MH327860	–	MH327898	MH327887

Table 3 (cont.)

Species	Strain[1]	Host and substrate	Locality	GenBank accession numbers[2]					
				SSU	ITS	LSU	*act1*	*tub2*	*tef1*
S. obovoideum	GUCC 18246*	Isolated from forest litter	China	**MZ503658**	**MZ503732**	**MZ503765**	**MZ546841**	**MZ546911**	**MZ546878**
S. olivaceum	CBS 137170*	Man, bronchoalveolar lavage fluid	USA: Utah	LM644548	LM644521	LM644564	LM644600	LM644605	KT272067
S. pandanicola	CBS 140660*	*Pandanus utilis*, leaves	France	–	KT950850	KT950864	–	–	–
S. phaeophorum	CBS 206.96*	Leaf in coastal rain forest	Papua New Guinea	KP798637	KP798631	KP798634	KT272054	KT272062	KT272098
S. podocarpi	CBS 143174*	*Podocarpus grayae*, leaves	Australia	–	MG386032	MG386085	–	–	MG386162
S. podocarpicola	CBS 146057*	Leaves of *Podocarpus latifolius*	South Africa	–	MN562138	MN567645	–	–	–
S. ramosum	CBS 137173*	Isolated from nail of *Homo sapiens*	USA: California	LM644551	LM644524	LM644567	LM644603	LM644608	KT272069
	CBS 137171	Skin	United States	LM644549	LM644522	LM644565	LM644601	LM644606	KT272068
	GUCC 18261	From forest litter	China	**MZ503673**	**MZ503747**	**MZ503780**	**MZ546856**	**MZ546926**	**MZ546893**
	GUCC 18262	From soil	China	**MZ503674**	**MZ503748**	**MZ503781**	**MZ546857**	**MZ546927**	**MZ546894**
	GUCC 18263	From forest litter	China	**MZ503675**	**MZ503749**	**MZ503782**	**MZ546858**	**MZ546928**	**MZ546895**
S. robustum	CBS 112.97*	Leaf litter of *Quercus ilex*	Spain	KP798639	KP798633	KP798636	KT272052	KT272060	KT272071
S. sexuale	CBS 135765*	Swabs in a laboratory	South Africa	KF156089	KF156018	KF156118	KF155902	KF156189	KF155976
	CBS 131965	Ant	Brazil	KF156090	KF156017	KF156119	KF155903	KF156188	KF155977
S. terreum	CBS 203.27*	From soil	USA: Louisiana	–	HQ667544	–	–	HQ877665	–
S. tshawytschae	CBS 100438*	On young *Oncorhynchus tshawytscha*	USA: California	KF156062	HQ667562	KF156126	KF155918	KF156180	KF155990
	CBS 228.66	Peat-bog soil	Ireland	KF156064	KF156016	KF156128	KF155915	KF156179	KF155992
	GUCC 18251	From lawn soil	China	**MZ503663**	**MZ503737**	**MZ503770**	**MZ546846**	**MZ546916**	**MZ546883**
	GUCC 18252	From plant litter	China	**MZ503664**	**MZ503738**	**MZ503771**	**MZ546847**	**MZ546917**	**MZ546884**
	GUCC 18253	From soil	China	**MZ503665**	**MZ503739**	**MZ503772**	**MZ546848**	**MZ546918**	**MZ546885**
	GUCC 18254	From soil	China	**MZ503666**	**MZ503740**	**MZ503773**	**MZ546849**	**MZ546919**	**MZ546886**
S. variabile	NBRC 32268	From soil	Canada: Ontario	EU107353	DQ307334	EU107310	–	–	DQ307356
S. verrucaria	GUCC 18240*	From soil	China	**MZ503652**	**MZ503726**	**MZ503759**	**MZ546835**	**MZ546905**	**MZ546872**
S. verrucosum	CBS 383.81*	From soil	India: Kerala	KF156067	KF156015	KF156129	KF155910	KF156185	KT272099
S. zunyiense	GUCC 18241*	From forest litter	China	**MZ503653**	**MZ503727**	**MZ503760**	**MZ546836**	**MZ546906**	**MZ546873**
V. calidifluminalis	CBS 125818*	Water of a hot stream	Japan	KF156046	AB385698	KF156108	KF155901	KF156202	KF155959
	CBS 125817	Water of a hot stream	Japan	KF156045	AB385699	KF156107	KF155900	KF156201	KF155958
V. cylindricalis	GUCC 18299*	From forest humus	China	**MZ503680**	**MZ503754**	**MZ503787**	**MZ546863**	**MZ546933**	**MZ546900**
V. gallopava	CBS 437.64*	*Meleagris gallopavo*, brain abscess	United States	KF156053	HQ667553	KF156112	HQ916989	KF156203	KF155968
	CBS 118.91	Man	United States	KF156047	HQ667551	KF282655	KF155932	HQ877643	JF440539
	CBS 867.95	Sputum from patient with cardiac	United States	KF156051	HQ667561	KF282657	KF155928	KF156213	KF155972
	CBS 116660	Human, transplantation	United States	KF156048	HQ667557	KF156115	KF155929	KF156206	KF155969
V. hainanensis	YMF1.04165*	From leaves of a dicotyledonous plant	China	MK248267	MK244397	MK248269	MK248271	–	MK248272
V. heveae	MFLUCC 17-0092*	On dried latex on bark of *Hevea brasiliensis*	Thailand	–	MH602349	MH602348	–	–	–
V. mangrovei	NFCCI-4390*	On decaying wood of *Excoecaria agallocha*	India	MN241147	MN782361	MN241144	–	MN848140	–
	NFCCI-4391	On decaying wood of *Excoecaria agallocha*	India	MN241148	MN782362	MN241145	–	MN848141	–
V. panacis	CBS 142802*	From the root of *Panax notoginseng*	China	MF536879	MF536882	MF536880	–	MF536883	MF536881
V. pseudotricladiata	YMF1.04915*	Leaves of a broad-leaf species in a stream	China	MK248268	MK244396	MK248270	–	MK253013	MK248273
V. terricola	CBS 131795*	Isolated from soil	China	–	MK810925	MK810811	–	–	–
V. thailandica	CBS 145768*	From soil	Thailand	–	MN794375	MN794352	–	–	–
	GUCC 18267	Isolated from the humus soil in the stream	China	**MZ503679**	**MZ503753**	**MZ503786**	**MZ546862**	**MZ546932**	**MZ546899**
V. tricladiata	NBRC 30208	On rotten leaves	Bismarck Archipelago	EU107354	–	EU107286	–	–	DQ307352
V. verruculosa	CBS 119775*	Grassland soil	India	KF156055	KF156014	KF156106	KF155919	KF156193	KF155974
Pseudosigmoidea excentrica	CBS 469.95*	*Lauraceae*, leaf litter	Cuba	KF156096	HQ667543	KF282669	KF155934	MK926478	KF155975
Sympoventuria capensis	CBS 120136*	*Eucalyptus* sp., leaf litter	South Africa	KF156094	MK810921	MK810808	–	MK926481	MK888745

[1] CBS: Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CPC: Culture collection of Pedro Crous, housed at Westerdijk Fungal Biodiversity Institute; CGMCC: Chinese General Microbiological Culture Collection Center, Beijing, China; GUCC: Culture Collection of the Department of Plant Pathology, Agriculture College, Guizhou University, China; HGUP: Herbarium of the Department of Plant Pathology, Agricultural College, Guizhou University, China; ICMP: International Collection of Micro-organisms from Plants, Landcare Research, Private Bag 92170, Auckland, New Zealand; IRAN: Fungal Culture Collections of the Iranian Research Institute of Plant Protection; MFLU (CC): Mae Fah Luang University Culture Collection, Chiang Ria, Thailand; MUCL: Universite Catholique de Louvain, Louvain-la-Neuve, Belgium. MTCC: Institute of Microbial Technology, Chandigarh, India; NBRC: Biological Resource Center; NFCCI: National Fungal Culture Collection of India, Pune, India.

[2] ITS: internal transcribed spacers and intervening 5.8S nrDNA; LSU: partial large subunit (28S) nrRNA gene; SSU: partial small subunit (18S) nrRNA gene; *act1*: actin; *tub2*: partial β-tubulin gene; *tef1*: partial translation elongation factor 1-alpha gene; *rpb2*: partial DNA-directed RNA polymerase II second largest subunit gene. Accession numbers of sequences generated in this study are in **bold**; – indicates unavailable sequences or unknown collection data.

* Ex-holotype or ex-type strains.

TreeBASE (Submission ID S29226), and all the sequences used for phylogenetic analysis are shown in Table 2 and 3.

Phylogenetic analyses

The concatenated DNA sequence dataset (SSU, ITS, LSU, *act1*, *tub2*, *tef1* and *rpb2*) of 143 taxa was used to infer phylogenetic relationships among the new isolates and other taxa of *Sympoventuriaceae*. DNA sequence data were initially blast searched to determine the placement of new strains in *Sympoventuriaceae*. Multiple sequence alignments were carried out with MAFFT v. 7.4.9 (Rozewicki et al. 2019), and then rechecked and adjusted manually as necessary using BioEdit v. 7.1.9 (Hall 1999). The single gene datasets were combined using MEGA X (Kumar et al. 2018). Data were converted from fasta to nexus and phylip format with AliView v. 1.19 for RAxML, MrBayes and PAUP analysis (Larsson 2014). Finally, phylogenetic analyses for the individual data matrix and combined datasets were conducted by employing maximum likelihood (ML), maximum parsimony (MP) and Bayesian inference (BI).

The ML analyses used RAxML-HPC2 on XSEDE v. 8.2.12 (Stamatakis 2014) via the CIPRES Science Gateway platform (Miller et al. 2012). The GTRGAMMA model was chosen and ML bootstrap analyses were estimated with 1 000 replicates. Prior to Bayesian analysis, jModelTest v. 2.1.7 (Darriba et al. 2012) was used to select a best-fit model of nucleotide substitution for each data partition under the output strategy of Akaike information criterion (AIC) (Nylander 2004). The Bayesian posterior probabilities were determined by Markov Chain Monte Carlo sampling (MCMC) in MrBayes v. 3.2.7 (Ronquist et al. 2012). The six simultaneous Markov chains were run for 2 M generations, starting from random trees and sampling trees every 100th generation, and 25 % of ageing samples were discarded, running until the average standard deviation of the split frequencies dropped below 0.01. For MP, the dataset was analysed in PAUP v. 4.0b10 (Swofford 2003) using a heuristic search algorithm with 1 000 random addition sequence replicates. One tree was saved at each step during stepwise addition, while tree bisection reconnection (TBR) was used to swap branches, and the maximum number of trees was set to 10 000. The ambiguously aligned regions were eliminated and gaps were treated as missing data. The phylogenetic trees were visualised in FigTree v. 1.4.4 and edited using Adobe Illustrator CC 2020.

Estimating transitions in lifestyle evolution

Ancestral character states of the lifestyle (Table 2, 3) were reconstructed with the Bayesian Binary Method (BBM) of RASP v. 4.2 (Yu et al. 2015, 2020). Because BBM analysis requires a set of phylogenetic trees and a consensus topology, we generated the phylogenetic trees via Bayesian phylogenetic analysis in BEAST v. 2.6.6 (Barido-Sottani et al. 2018) using six DNA loci (SSU, ITS, LSU, *act1*, *tub2* and *tef1*). The length of the MCMC chain reaction was set as 500 M generations sampled every 100 000 generations; thus, a total of 5 000 trees were kept. Tracer v. 1.7.2 (Rambaut et al. 2018) was used to check that the values of the mean and ESS in the log file were over 200. After removal of a proportion of each run as burn-in, the remaining trees were summarised as maximum clade credibility (MCC) trees in TreeAnnotator v. 2.6.6 (Barido-Sottani et al. 2018). For BBM analysis, the Markov chains were run for 50 000 generations, using 10 chains, with a sample frequency of 100, a temperature of 0.1, state frequencies fixed (JC), and among-site rate variation equal. We subsequently examined the resulting reconstructions of the selected characters to determine if the lifestyle changes were arising convergently or resulted from shared ancestry.

Morphological observations

The microscopic features and colony characteristics of the putative novel and known species were examined. The macromorphological characters and relevant data (colony colour and diameter, mycelium) of the isolates were examined under a dissecting microscope (Leica S9i, Germany), and images of colonies cultured on three media, malt extract agar (MEA), oatmeal agar (OA) (Crous et al. 2019b) and PDA were captured after 2 wk. The slide culture technique on OA was used for microscopic observation. If sterile on OA, morphological characters produced on other media were described. Measurements and descriptions of reproductive structures were taken from specimens mounted in lactic acid or lactophenol cotton blue. Micrographs were captured with an Olympus BX53 compound microscope. Tarosoft (R) Image Frame Work program was used to measure the lengths and widths of microscopic structures including conidiophores, conidiogenous cells, conidia and chlamydospores per isolate. At least 30 measurements were made for each microscopic structure to calculate the mean value, standard deviation, and minimum–maximum values, with the extreme measurements in parentheses (Giraldo & Crous 2019, Fan et al. 2020, Liu et al. 2022). Descriptions are based on observations after 14 d of incubation at 26 °C. Slow-growing species were allowed to grow longer, for 20–30 d, until sporulation was observed.

RESULTS

Phylogenetic analyses

For the two datasets in the present study (Table 2, 3), phylogenetic analyses obtained from ML, MP and BI analyses resulted in trees with similar topologies, and the best scoring ML tree was selected to represent and discuss the phylogenetic relationships among taxa (Fig. 1, 2). *Sympoventuriaceae* phylogeny (Fig. 1): the first tree was based on a concatenated DNA sequence dataset (ITS, LSU, *tef1*, *tub2* and *rpb2*) used to infer the phylogenetic position of the treated genera and species within the *Sympoventuriaceae*. The sequence data comprised 69 taxa for *Sympoventuriaceae* with *Tyrannosorus lichenicola* and *Venturia saliciperda* as the outgroup taxa. The dataset consisted of 5 175 characters, of which 2 399 were constant, 2 173 parsimony-informative and 603 parsimony-uninformative. Based on the results of the jModelTest, GTR+I+G was estimated as the optimal nucleotide substitution model under the output strategy of AIC; *Scolecobasidium* and *Verruconis* phylogeny (Fig. 2): for the sake of revealing the phylogenetic relationship between *Scolecobasidium* and *Verruconis* species, a second analysis was performed on the six gene regions (ITS, LSU, SSU, *act1*, *tub2* and *tef1*) of 97 taxa within the genus, and *Pseudosigmoidea excentrica* and *Sympoventuria capensis* were used as outgroups. The final aligned sequence matrix contained 5 919 characters, of which 3 054 were constant, 2 152 parsimony-informative and 713 parsimony-uninformative. The optimal nucleotide substitution model HKY+I+G was used for the phylogenetic analyses.

The phylogenetic tree of *Sympoventuriaceae* distinguished 22 subclades, each subclade representing a highly supported monophyletic group (Fig. 1). *Acroconidiellina* was located at the terminal end of the phylogenetic tree, closely related to *Scolecobasidium* and *Verruconis* (Fig. 1). Phylogenetic analyses resolved 43 species of *Scolecobasidium*, which chiefly clustered in five subclades, of which 37 correspond to known species of the genus (Fig. 2). In the *Verruconis* lineage three major subclades were observed, corresponding closely to the currently recognised 11 species (Fig. 2). The 29 newly collected strains clustered in eight well-supported subclades of

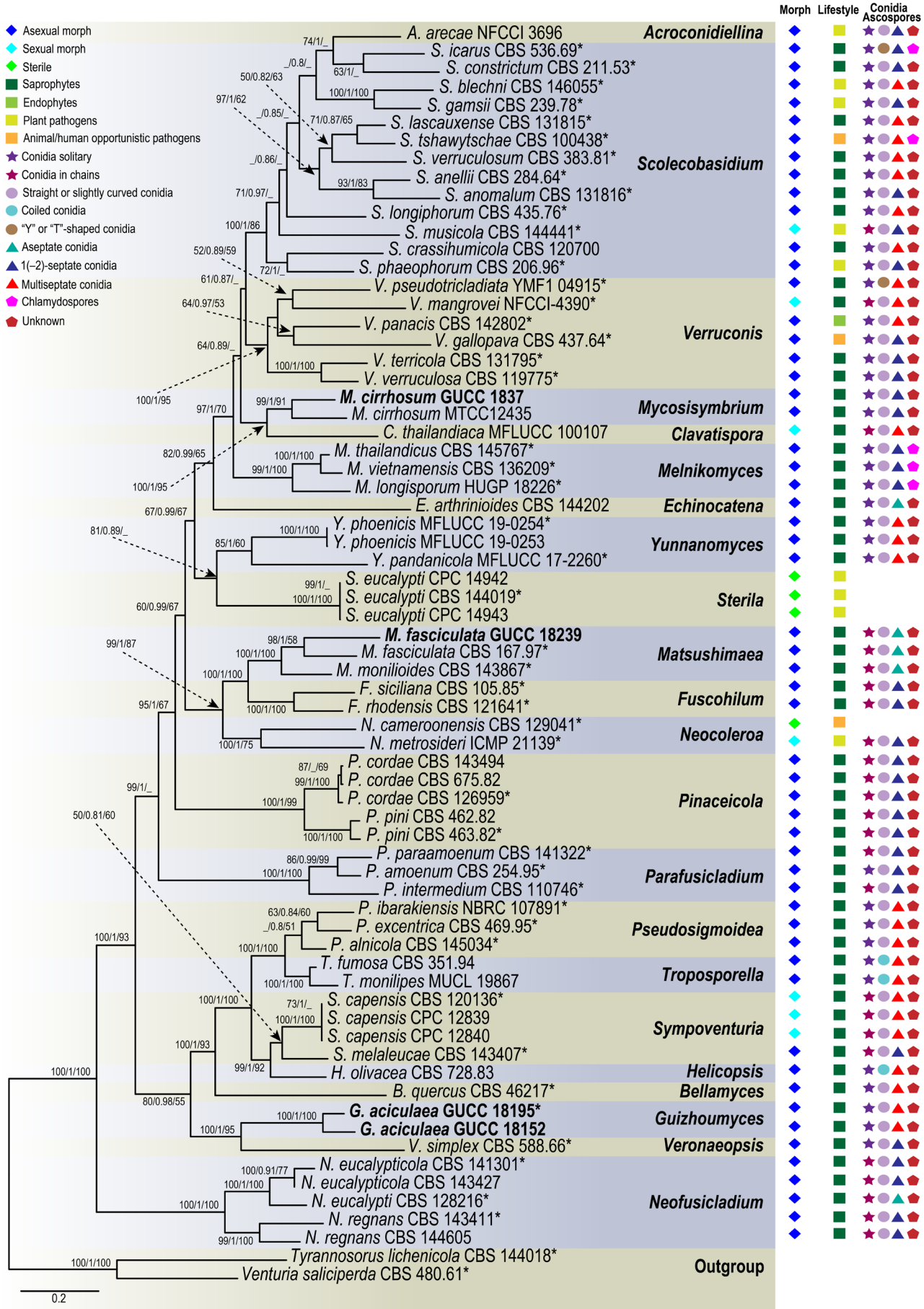

Fig. 1 Phylogenetic tree of the family *Sympoventuriaceae* based on RAxML analyses of combined DNA dataset of ITS, LSU, *tef1*, *tub2* and *rpb2* gene sequences. Bootstrap values ≥ 50 % for Maximum parsimony and Maximum likelihood, and Bayesian posterior probabilities ≥ 80 % are presented at the branches (ML/BI/MP). Some branches were shortened to facilitate layout, and the scale bar represents the number of changes. *Tyrannosorus lichenicola* and *Venturia saliciperda* are used as outgroup. Those in **bold** are new taxa or new combinations proposed in the current study and the strains obtained, as well as type strains are marked with an asterisk (*). Lifestyles and typical morphological characteristics of individual strains are shown at the right side of the phylogenetic tree, and the related icons plotted are explained in the legend in the upper left corner.

Scolecobasidium and *Verruconis* respectively, including seven new species, as well as six new combinations proposed here (Fig. 2). The monotypic genus *Mycosisymbrium* consisted of two highly supported clades, which can be distinguished from other genera in this family, and *Clavatispora* as the sister genus (Fig. 1). Three clades were distinguished in *Melnikomyces*, corresponding closely to the currently recognized three species (*M. longisporus*, *M. thailandicus* and *M. vietnamensis*), which are saprophytes in soil or plant debris (Fig. 1). *Echinocatena*, a monotypic genus represented by *E. arthrinioides*, formed a robust lineage at the base of the *Melnikomyces* (Fig. 1). *Sterila* and *Yunnanomyces* clustered in the same subclade and received moderate to strong support, which was divided into two clades; the first one included the ex-type strain of *Y. pandanicola* and two *Y. phoenicis* strains, and the second one included three sterile strains (*S. eucalypti*) (Fig. 1).

Fuscohilum, *Matsushimaea* and *Neocoleroa* grouped together and represent three monophyletic groups; the first group comprising *F. rhodense* and *F. sicilianum*, the second group *M. fasciculata* and *M. mtonilioides*, and the third group *N. cameroonensis* and *N. metrosideri*, which are plant, animal and human pathogens (Fig. 1). *Pinaceicola* (*P. cordae* and *P. pini*) and *Parafusicladium* (*P. amoenum*, *P. intermedium* and *P. paraamoenum*) formed a well circumscribed clade (Fig. 1). *Pseudosigmoidea* included *P. alnicola*, *P. excentrica* and *P. ibarakiensis*, which formed a robust clade with four other genera, viz.,

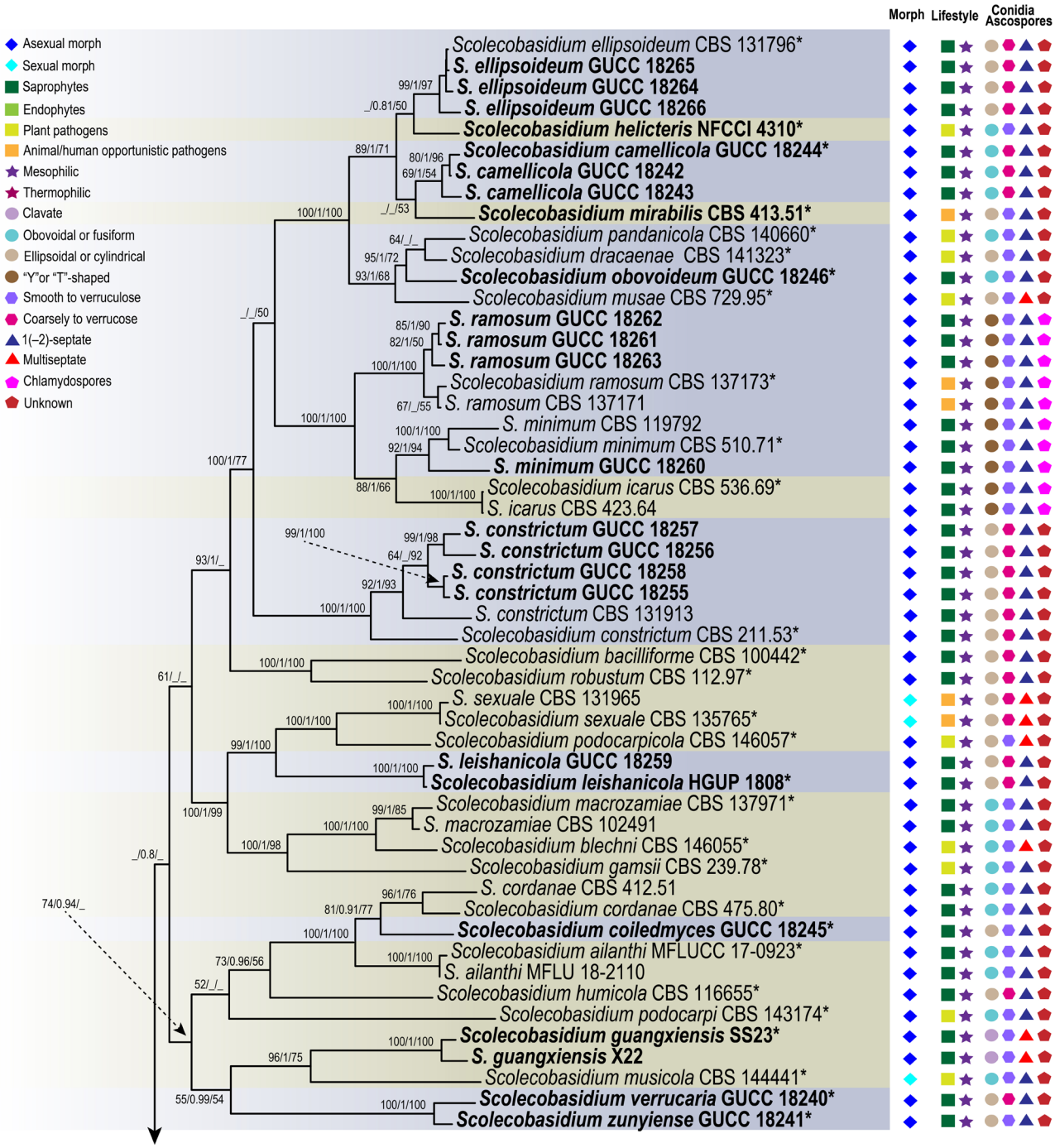

Fig. 2 Phylogenetic tree of the genera *Scolecobasidium* and *Verruconis* based on RAxML analyses of combined DNA dataset of SSU, ITS, LSU, *act1*, *tub2* and *tef1* gene sequences. Bootstrap values ≥ 50 % for Maximum parsimony and Maximum likelihood, and Bayesian posterior probabilities ≥ 80 % are presented at the branches (ML/BI/MP). Some branches were shortened to facilitate layout, and the scale bar represents the number of changes. *Pseudosigmoidea excentrica* and *Sympoventuria capensis* are used as outgroup. Those in **bold** are new taxa or new combinations proposed in the current study and the strains obtained, as well as type strains are marked with an asterisk (*). Lifestyles and typical morphological characteristics of individual strains are shown at the right side of the phylogenetic tree, and the related icons plotted are explained in the legend in the upper left corner.

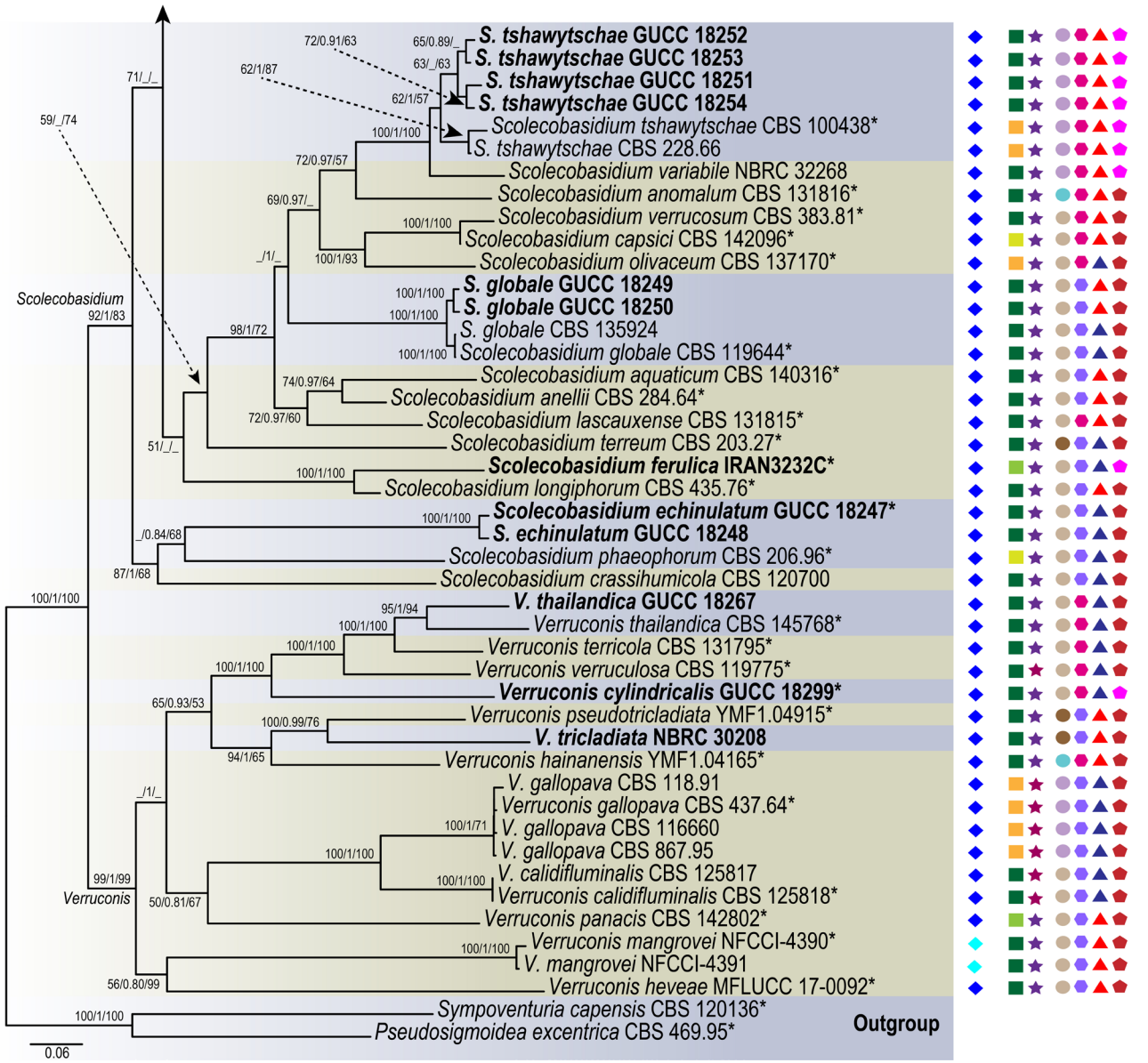

Fig. 2 (cont.)

Bellamyces, *Helicopsis*, *Sympoventuria* and *Troposporella* (Fig. 1). However, the phylogenetic relationship of these genera with the other clades remains poorly unresolved. *Guizhoumyces* belongs to a monophyletic clade, together with *Veronaeopsis*, representing a new genus in *Sympoventuriaceae* (Fig. 1). *Neofusicladium* encompassed three highly statistically supported subclades at the base of *Sympoventuriaceae*, which represent *N. eucalypti*, *N. eucalypticola* and *N. regnans*, respectively (Fig. 1). Relationships of the new taxa are discussed in the notes.

Lifestyle evolution analysis

Ancestral states of the lifestyles in *Sympoventuriaceae* were inferred on the reconstructed phylogeny. We defined the life strategies in four states: saprophytes, endophytes, plant pathogens, and animal/human opportunistic pathogens. Overall, the results of BBM analysis revealed that the life strategies of *Sympoventuriaceae* was based on saprophytes as the primitive state, and endophytes, plant pathogens, animal/human opportunistic pathogens were derived states, correlating with phylogeny (Fig. 3). At the genus level, *Bellamyces*, *Echinocatena*, *Guizhoumyces*, *Helicopsis*, *Neofusicladium*, *Parafusicladium*, *Pseudosigmoidea*, *Sympoventuria*, *Troposporella* and *Veronaeopsis* were basal in *Sympoventuriaceae* with a saprotrophic lifestyle, correlating with their ecology. The recently introduced *Sterila* and *Neocoleroa* were strongly supported as ingroup taxa of *Sympoventuriaceae*, and have evolved from saprophytes to become plant pathogens (for *S. eucalypti* and *N. metrosideri*) or animal/human opportunistic pathogens (for *N. cameroonensis*) (Fig. 3). However, these lifestyles reverted to saprotrophic again in the well-supported *Clavatispora*, *Fuscohilum*, *Matsushimaea*, *Melnikomyces* and *Mycosisymbrium* clades. In the *Acroconidiellina*, *Scolecobasidium* and *Verruconis* clades, the number of plant pathogens and animal or human opportunistic pathogens increased from *Sterila* (one species) to *Acroconidiellina* (one species), *Scolecobasidium* (16 species) and *Verruconis* (one species), whereas the transition to endophytes occurred only twice in *Scolecobasidium* and *Verruconis*, respectively (Fig. 3). Thus, we conclude that the outstanding diversification of *Scolecobasidium* is related to the evolution of derived life strategies, and that the lifestyle of this genus may have been influenced by both plants and animals. Moreover, the common ancestor of the other genera except for *Acroconidiellina*, *Neocoleroa* and *Sterila* was saprophytic (Fig. 3), which is a derived condition from a saprotrophic ancestor of *Sympoventuriaceae*.

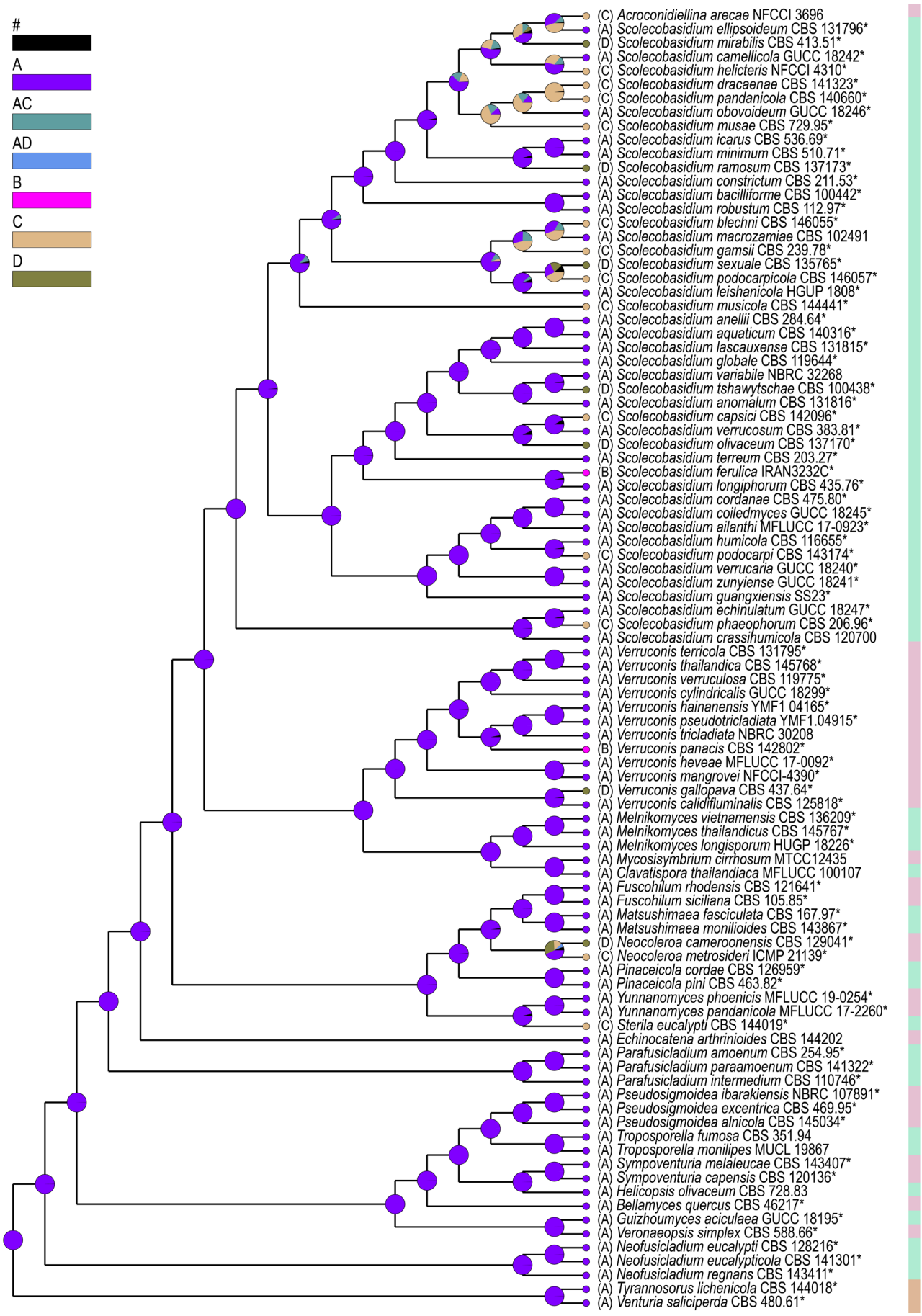

Fig. 3 Ancestral character state analysis focusing on lifestyles in *Sympoventuriaceae*, using Bayesian Binary MCMC as alternative method. The pie chart at each node indicates the relative probabilities of all possible ancestral states from the Bayesian analysis, and black (#) shows the pooled probabilities of estimates that each account for < 5 %. Coloured circles at the tip and letters next to taxa represent their current lifestyle. A. saprophytes; B. endophytes; C. plant pathogens; D. animal/human opportunistic pathogens. The type strains are marked with an asterisk (*). *Tyrannosorus lichenicola* and *Venturia saliciperda* are used as outgroup.

Table 4 Genera accepted in *Sympoventuriaceae*.

Zhang et al. (2011)	Wijayawardene et al. (2014)	Tibpromma et al. (2018)	Wijayawardene et al. (2020)	Shen et al. (2020)	This study (2022)
Fusicladium-like	*Clavatispora*	*Fusicladium*	*Acroconidiellina*	*Bellamyces*	*Acroconidiellina*
Sympoventuria	*Ochroconis*	*Ochroconis*	*Clavatispora*	*Echinocatena*	*Bellamyces*
Veronaeopsis	*Sympoventuria*	*Sympoventuria*	*Fusicladium*	*Fuscohilum*	*Clavatispora*
	Veronaeopsis	*Scolecobasidium*	*Matsushimaea*	*Helicopsis*	*Echinocatena*
		Veronaeopsis	*Mycosisymbrium*	*Neocoleroa*	*Fuscohilum*
		Verruconis	*Ochroconis*	*Neofusicladium*	*Guizhoumyces*
		Yunnanomyces	*Sympoventuria*	*Pseudosigmoidea*	*Helicopsis*
			Veronaeopsis	*Parafusicladium*	*Matsushimaea*
			Verruconis	*Pinaceicola*	*Melnikomyces*
			Yunnanomyces	*Sympoventuria*	*Mycosisymbrium*
				Scolecobasidium	*Neocoleroa*
				Sterila	*Neofusicladium*
				Troposporella	*Pseudosigmoidea*
				Veronaeopsis	*Parafusicladium*
				Verruconis	*Pinaceicola*
					Sympoventuria
					Scolecobasidium
					Sterila
					Troposporella
					Veronaeopsis
					Verruconis
					Yunnanomyces

TAXONOMY

Sympoventuriaceae Y. Zhang ter et al., Fungal Diversity 51: 255. 2011

Type genus. *Sympoventuria* Crous & Seifert.

Notes — *Sympoventuriaceae* was established by Zhang et al. (2011) with *Sympoventuria* designated as the type genus, which can be distinguished from the *Venturiales* by its saprophytic lifestyle, presence of pseudoparaphyses, and hyaline, symmetrical ascospores (Arzanlou et al. 2007, Crous et al. 2007a, b, Zhang et al. 2011). Phylogenetically, *Sympoventuriaceae* forms a well-supported family clade within *Venturiales* (Zhang et al. 2011, Machouart et al. 2014). Subsequently, Hyde et al. (2013) recognised three lineages (i.e., *Sympoventuria*, *Veronaeopsis* and fusicladium-like species) within *Sympoventuriaceae* and provided more details. Over the past few years, more genera have been accepted in *Sympoventuriaceae*, such as *Ochroconis*, *Scolecobasidium* and *Verruconis* (Machouart et al. 2014). The taxonomy of *Sympoventuriaceae* has since been widely studied and dramatically changed (Wijayawardene et al. 2014, Tibpromma et al. 2018). Despite these changes, the phylogenetic placement of many genera in the *Sympoventuriaceae* remains to be elucidated. Shen et al. (2020) re-described *Sympoventuriaceae* based on a multigene phylogenetic analysis, morphological and ecological comparisons, and included 15 genera in this family. However, generic boundaries within *Sympoventuriaceae* are poorly resolved and still controversial, due to lack of type materials and unresolved phylogenies. In this study, we accept 22 genera in *Sympoventuriaceae* (Fig. 1, Table 4).

Guizhoumyces T.P. Wei & Y.L. Jiang, *gen. nov.* — MycoBank MB 840922

Etymology. Named after Guizhou, where this species was collected and the Greek name for fungi (myces).

Type species. *Guizhoumyces hyalinaea* T.P. Wei & Y.L. Jiang.

Mycelium consisting of curved or straight, branched, pale brown, septate, smooth-walled hyphae, frequently forming hyphal coils. *Conidiophores* subcylindrical, simple, branched, straight or slightly geniculate, pale brown, smooth, septate, sometimes reduced to conidiogenous cells. *Conidiogenous cells* integrated, simple, polyphialidic, sympodially proliferating, elongate lageniform or ampulliform, terminal or intercalary, pale brown, with an inconspicuous or distinct denticle at the conidiogenous locus after rhexolytic conidial secession. *Conidia* enteroblastic, solitary, acicular to obclavate or cylindrical, septate, straight or somewhat curved, smooth, thin-walled, subhyaline to pale brown, apex subobtuse to pointed, base truncate to short obconically truncate, with thickened and darkened hilum; anastomosis between mature conidia. *Chlamydospores* were not observed and *sexual morph* unknown.

Notes — The genus *Guizhoumyces* was established to accommodate a new species *G. aciculaea*. The phylogeny of concatenated ITS, LSU, *rpb2*, *tef1* and *tub2* DNA sequences indicated that *Guizhoumyces* formed a fully supported monophyletic lineage in *Sympoventuriaceae*, which is sister to *Bellamyces*, *Helicopsis*, *Sympoventuria* and *Veronaeopsis*. Morphologically, this genus has certain similarities with *Pseudosigmoidea* and *Sigmoidea*, but can be distinguished from them by its acicular to obclavate or cylindrical, less than four septate and smaller conidia (Crane 1968, Ando & Nakamura 2000, Crous et al. 2019a). Therefore, based on its unique morphological characteristics and phylogenetic location, a new genus name *Guizhoumyces* is introduced to accommodate this new fungus.

Guizhoumyces aciculaea T.P. Wei & Y.L. Jiang, *sp. nov.* — MycoBank MB 840923; Fig. 4

Etymology. The epithet refers to the acicular conidia.

Typus. China, Guizhou Province, Shiqian County, Pingshan Township, Fodingshan National Nature Reserve, N27°40'50" E108°07'30", 1100 m a.s.l., isolated from soil, 2 Nov. 2019, *T.P. Wei* (holotype HGUP 18195, isotype CGMCC 3.20543, culture ex-type GUCC 18195).

Mycelium consisted of branched, pale brown, septate, thick-walled, 2–3 µm diam hyphae, frequently forming hyphal coils. *Conidiophores* mostly flask-shaped to subcylindrical, simple, straight or slightly geniculate, pale brown, smooth, septate, sometimes reduced to conidiogenous cells, (10–)13–46.5(–48) × 1.5–2.5(–3) µm (av. ± SD = 25.5 ± 12.7 × 2.1 ± 0.4 µm,

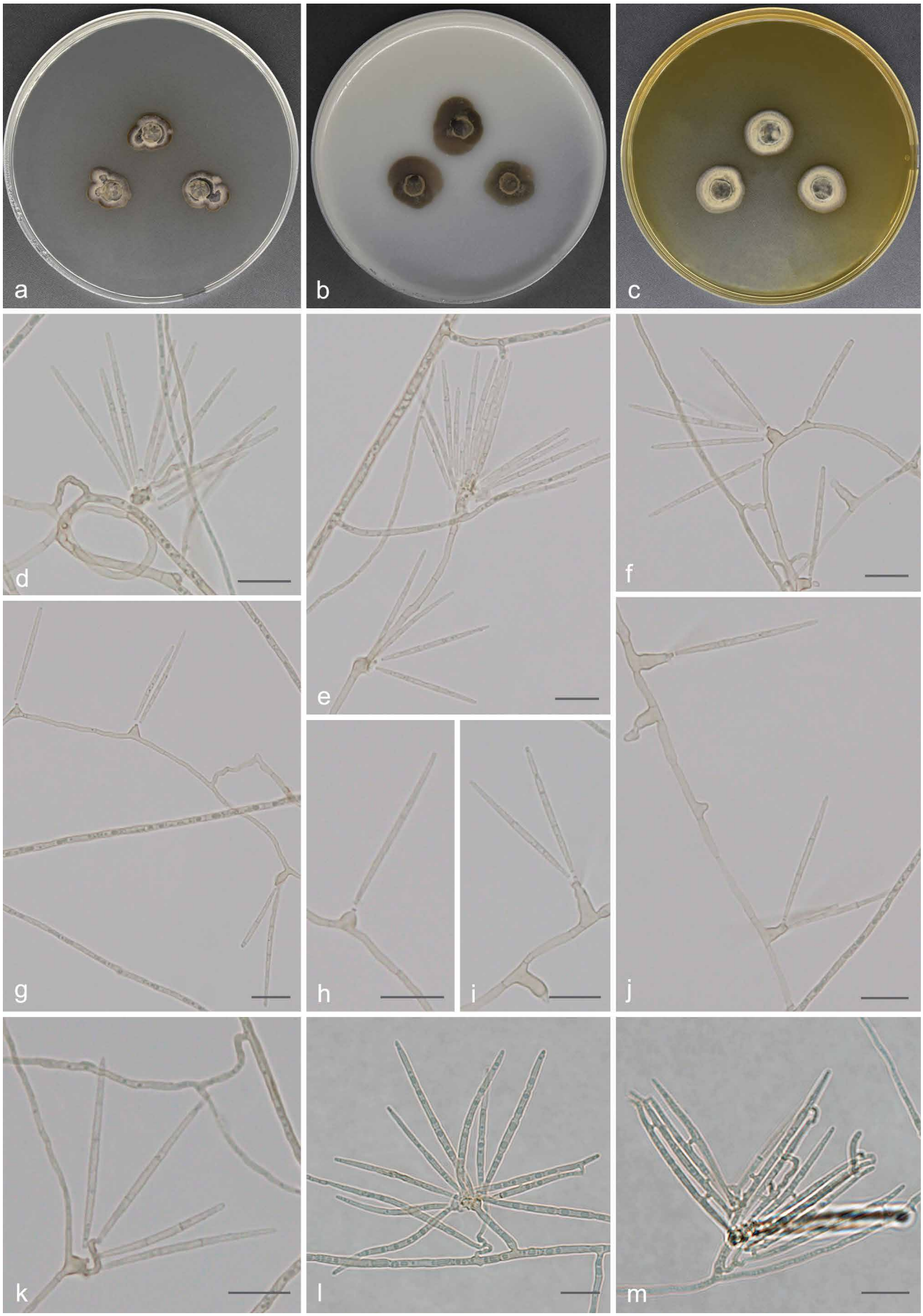

Fig. 4 *Guizhoumyces aciculaea* (culture ex-type GUCC 18195). a–c. Colony on PDA, OA and MEA; d. hyphal coils and conidia; e–j. conidiophores reduced to conidiogenous cells; k–l. conidiophores with conidiogenous cells and conidia; m. anastomosis between mature conidia. — Scale bars: d–m = 10 µm.

n = 30). *Conidiogenous cells* integrated, simple, polyphialidic, sympodially proliferating, elongate lageniform or ampulliform, terminal or intercalary, pale brown, 4–12(–15.5) × 2–3.5 µm (av. ± SD = 7.8 ± 2.7 × 2.7 ± 0.4 µm, n = 30), with one or numerous denticles in the apex, hyaline to pale brown, 1–3 µm long. *Conidia* separate rhexolytically from conidiogenous cells, enteroblastic, solitary, acicular to obclavate or cylindrical, 0(–3)-septate, straight or somewhat curved, smooth, thin-walled, subhyaline to pale brown, apex subobtuse to pointed, base truncate to short obconically truncate, with thickened and darkened hilum, anastomosis between mature conidia, (19.5–)21.5–37(–39.5) × 1.5–2 µm (av. ± SD = 27.8 ± 4.2 × 1.5 ± 0.1 µm, n = 30).

Culture characteristics — Colonies on PDA reaching up to 14–15 mm diam after 14 d at 26 °C, compact, surface grey brown, slightly raised at centre. On OA reaching 16–19 mm diam, with sparse aerial mycelium, olivaceous grey. On MEA reaching 14–16 mm diam, raised, hairy, with abundant aerial hyphae, grey at the surface, reverse pale brown.

Additional material examined. China, Guizhou Province, Shiqian County, Ganxi Township, Fodingshan National Nature Reserve, N27°40'51" E108°07'21", 1240 m a.s.l., from leaf litter, 10 June 2019, *T.P. Wei* (HGUP 18152), living culture GUCC 18152 = CGMCC 3.20542.

Notes — *Guizhoumyces aciculaea* somewhat resembles the type species *P. cranei* and *S. prolifera* of *Pseudosigmoidea* and *Sigmoidea* in conidial morphology, with enteroblastic conidiogenesis and phialidic conidiogenous cells, which would suggest that our taxon could be accommodated here. Unfortunately, *Pseudosigmoidea* and *Sigmoidea* (*Halosphaeriaceae*, *Microascales*) are distantly related to *G. aciculaea* (Fig. 1). Morphologically, *G. aciculaea* can also be distinguished from *P. cranei* and *S. prolifera*. The conidia of *P. cranei* are scolecoid, 3(–8)-septate and longer (29–116.5 × 1.5–2.5 µm) (Ando & Nakamura 2000); conidia of *S. prolifera* are scolecoid, 5(–11)-septate, hyaline and larger (44–110 × 2–2.5 µm) (Crane 1968). In contrast, *G. aciculaea* has acicular to obclavate or cylindrical, 0(–3)-septate, subhyaline to pale brown and smaller conidia (19.5–39.5 × 1.5–2 µm), and anastomosis occurs among mature conidia. Moreover, the ex-type culture of *G. hyalinaea* and *V. simplex* clustered in two distinct clades representing two different genera (Fig. 1). *Guizhoumyces hyalinaea* is clearly distinct from *V. simplex*, which has oblong to subcylindrical, 0(–1)-septate and very small conidia (6–15 × 2–4 µm) (Arzanlou et al. 2007).

Scolecobasidium E.V. Abbott, Mycologia 19: 30. 1927

Synonym. *Ochroconis* de Hoog & Arx, Kavaka 1: 57. 1974 '1973'.

Type species. *Scolecobasidium terreum* E.V. Abbott.

Notes — *Scolecobasidium* was first described by Abbott (1927) to accommodate *S. constrictum* and *S. terreum* isolated from cotton and sugarcane soils in Louisiana, USA, with *S. terreum* designated as the generic type, which has Y-shaped and yellowish conidia. The salient characters of *Scolecobasidium* are rust-brown to olivaceous colonies producing small, brownish conidiophores bearing small numbers of dark, septate, rough-walled, rhexolytic conidia (Abbott 1927, Ellis 1976). Abbott (1927) pointed out that *Scolecobasidium* is distinguished from other groups by the shape of its conidia and the way conidia are arranged on its conidiophores. In the following decades, this genus received unanimous support (Barron & Busch 1962, Roy et al. 1962, Graniti 1963). Later, more species with unbranched conidia were described within *Scolecobasidium*, which led De Hoog & Von Arx (1973) to introduce a separate genus, *Ochroconis*, typified by *O. constricta* for hyphomycetous species with unbranched, subspherical to cylindrical or clavate, melanised conidia (Matsushima 1975, 1980, Punithalingam & Spooner 2011). *Scolecobasidium* was restricted to species with T- or Y-shaped or bilobed, two- to multi-celled conidia (Martin-Sanchez et al. 2012). It is noteworthy that the ex-type strains of both *S. terreum* (CBS 203.27) and *O. constricta* (CBS 202.27) are now sterile (Horre et al. 1999, Gams 2015).

Samerpitak et al. (2014) revised *Ochroconis* and *Scolecobasidium* using SSU, ITS, LSU, *act1*, *tub2* and *tef1* DNA sequences. They found that *Ochroconis* and *Scolecobasidium* clustered together, while *Scolecobasidium* was considered as doubtful because the ex-type culture was sterile (Samerpitak et al. 2017). This opinion, however, was not shared by Gams (2015) who regarded *Ochroconis* as a synonym of *Scolecobasidium*, which was supported by Seifert et al. (2011). More recently, Shen et al. (2020) resolved *Ochroconis* as a synonym of *Scolecobasidium* based on the multi-locus (ITS, LSU, *tef1*, *tub2* and *rpb2*) analysis combined with morphology and ecology, with strong support for its monophyly. We agree with Shen et al. (2020) that *Solecobasidium* equals *Ochroconis*. As noted by Gams (2015) and Shen et al. (2020), although the ex-type strain of *S. terreum* is sterile, there are many reliably named cultures of *S. terreum* globally, which clearly define the identity of this characteristic fungus. *Scolecobasidium* will always be applied to the clade that includes the type species *S. terreum* and *O. constricta* of *Scolecobasidium* and *Ochroconis*. This study shows that the clade defined as *Scolecobasidium* combines monophyly, sexual and asexual morphs, and ecological characters in a coherent way that can logically be recognised at the generic rank. Additionally, many species of *Ochroconis* for which DNA data are available have since been transferred to *Scolecobasidium* by Shen et al. (2020), except *O. ferulica*, *O. guangxiensis*, *O. helicteris O. mirabilis* and *O. terricola*, which are discussed below.

Scolecobasidium camellicola T.P. Wei & Y.L. Jiang, *sp. nov.* — MycoBank MB 840926; Fig. 5

Etymology. The epithet refers to *Camellia*, the host genus from which this fungus was collected.

Typus. China, Guizhou Province, Meitan County, N27°75'09" E107°47'99", 910 m a.s.l., isolated from decaying *Camellia sinensis* leaf litter, 10 Aug. 2019, *T.P. Wei* (holotype HGUP 18242, isotype CGMCC 3.20547, culture ex-type GUCC 18242).

Mycelium partly superficial, partly immersed, hyphae branched, pale brown, septate, smooth, thick-walled, 1–2 µm wide. *Conidiophores* arising directly from superficial hyphae, mostly unbranched, subcylindrical, straight or flexuous, brown, continuous or septate, (10–)11.5–55(–61.5) × 2.5–4 µm (av. ± SD = 19.4 ± 13.7 × 2.6 ± 0.4 µm, n = 30). *Conidiogenous cells* integrated, polyblastic, intercalary or terminal, sympodial extensions, pale brown to brown, bearing 1–6 conidia at the apex, (6–)7.5–13(–14) × (2–)2.5–3.5 µm (av. ± SD = 9.2 ± 2.1 × 2.6 ± 0.4 µm, n = 30). *Conidia* secession rhexolytic from conidiogenous cells, subcylindrical or fusoid, 1-septate, minutely echinulate, pale brown, slightly constricted at the septum, with hilum bearing a marginal frill, (7–)7.5–10.5(–11.5) × (2.5–)3–4.5 µm (av. ± SD = 8.7 ± 0.9 × 3.4 ± 0.5 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 21–22 mm diam after 14 d at 26 °C, growing slow, isabelline, raised in the centre. On OA reaching up to 23–24 mm diam, flat, spreading, immersed, dark brown. On MEA reaching 22–24 mm diam, raised, with sparse to moderate aerial hyphae, pale to medium brown.

Additional materials examined. China, Guizhou Province, Meitan County, N27°75'09" E107°47'99", 910 m a.s.l., on decaying *Camellia sinensis* leaf litter, 10 Aug. 2019, *T.P. Wei* (HGUP 18243), living culture GUCC 18243 = CGMCC 3.20548; Leishan County, N26°24'02" E107°77'22", 1178 m a.s.l., from forest litter, 12 Mar. 2018, *T.P. Wei* (HGUP 18244), living culture GUCC 18244 = CGMCC 3.20549.

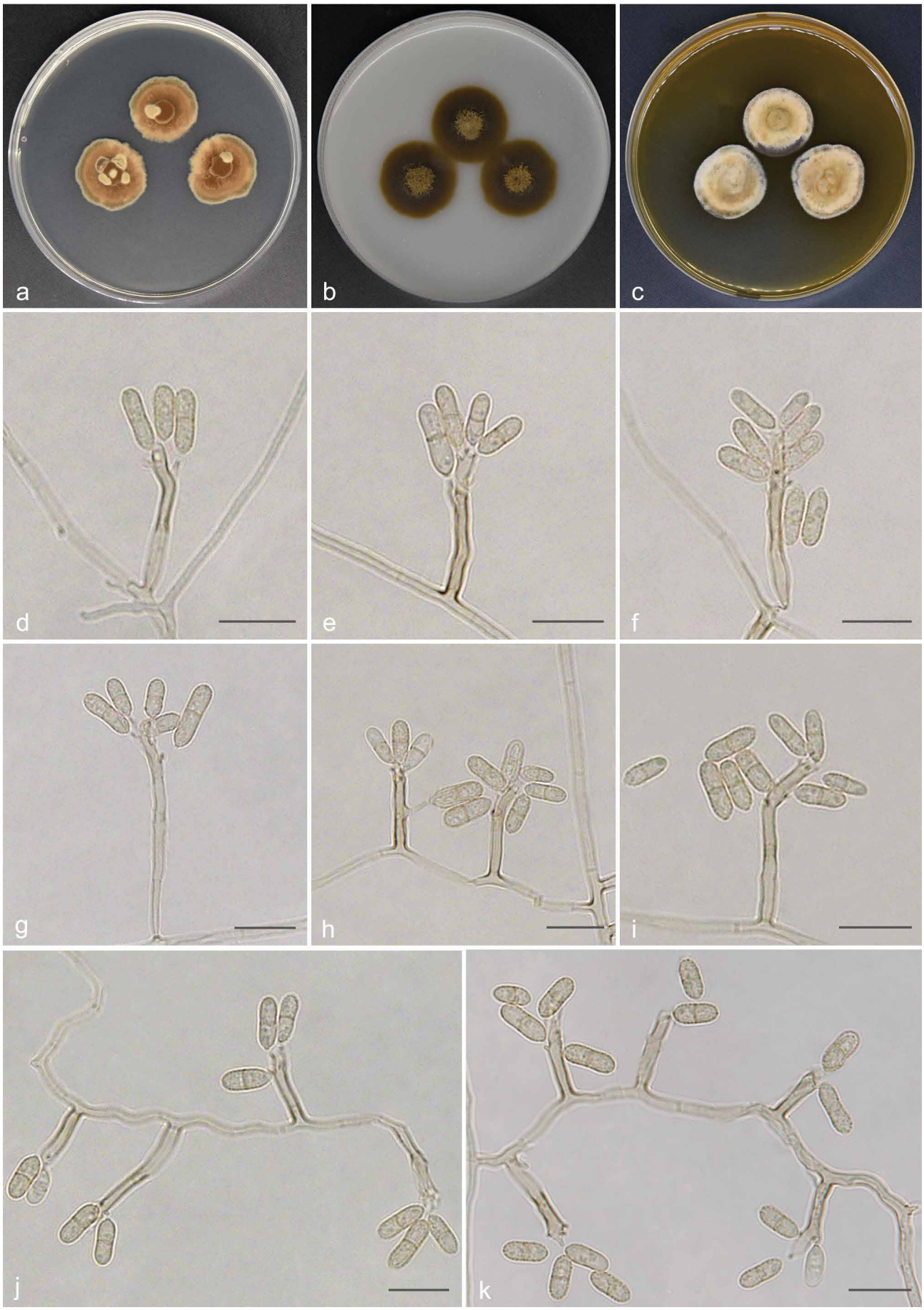

Fig. 5 *Scolecobasidium camellicola* (culture ex-type GUCC 18242). a–c. Colony on PDA, OA and MEA; d–h. conidiogenous cells giving rise to conidia; i. aging conidia forming conidiogenous loci; j–k. hypha with conidiogenous cells and conidia. — Scale bars: d–k = 10 µm.

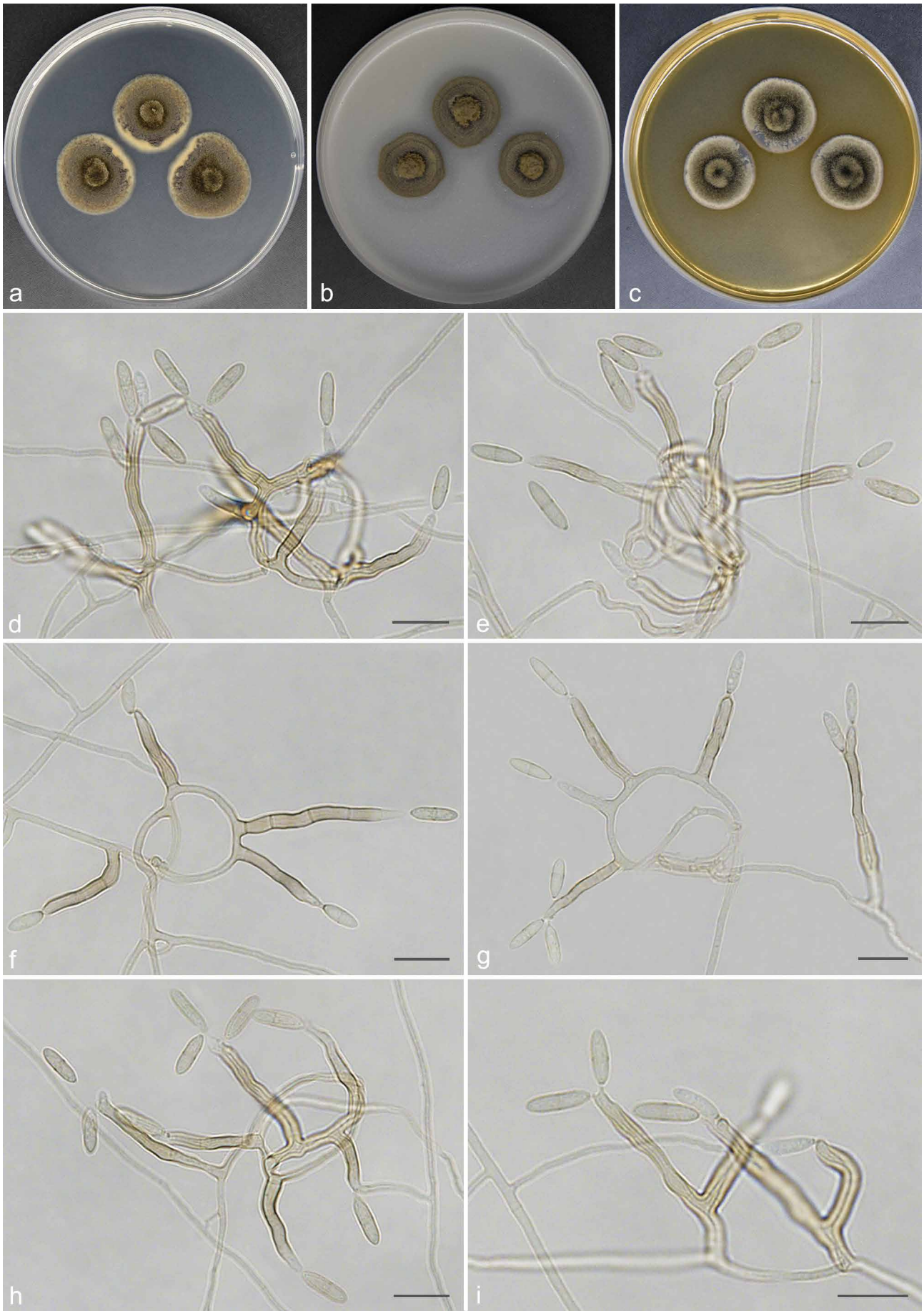

Fig. 6 *Scolecobasidium coiledmyces* (culture ex-type GUCC 18245). a–c. Colony on PDA, OA and MEA; d–g. conidiophores arising from hyphal coils; h. conidiophores with conidiogenous cells and conidia; i. branched conidiophores. — Scale bars: d–i = 10 µm.

Notes — *Scolecobasidium camellicola* is introduced as a new species based on morphological and phylogenetic differences to other *Scolecobasidium* species. Phylogenetically, *S. camellicola* shares a sister relationship with *S. mirabilis* and *S. helicteris* with high statistical support (Fig. 2). Nevertheless, *S. camellicola* showed high heterogeneity, forming a well-separated clade, which was genetically distant from all species. Morphologically, *S. mirabilis* differs from *S. camellicola* by its smooth-walled to verruculose and larger conidia (9.0–13.5 × 4.8–6.7 µm vs 7–11.5 × 2.5–4.5 µm) (Samerpitak et al. 2014); *S. helicteris* differs by its smooth to verruculose, ellipsoid or pyriform and smaller conidia (4–8 × 2–3.4 µm vs 7–11.5 × 2.5–4.5 µm) (Singh et al. 2019).

Scolecobasidium coiledmyces T.P. Wei & Y.L. Jiang, *sp. nov.* — MycoBank MB 840927; Fig. 6

Etymology. The epithet refers to the frequently forming hyphal coils.

Typus. China, Guizhou Province, Guiyang City, Huaxi Wetland Park, N26°43'92" E106°67'76", 1140 m a.s.l., isolated from lawn soil, 16 Nov. 2018, *T.P. Wei* (holotype HGUP 18245, isotype CGMCC 3.20550, culture ex-type GUCC 18245).

Mycelium consisting of smooth, septate, branched, subhyaline or medium brown, 1.5–3 µm diam hyphae, forming hyphal coils. *Conidiophores* erect, 0(–4)-septate, occasionally branched, brown to dark brown, smooth and thick walled, subcylindrical, (12–)13–43(–56) × 2.5–4(–4.5) µm (av. ± SD = 23.9 ± 9.5 × 3.1 ± 0.5 µm, n = 30). *Conidiogenous cells* terminal, subhyaline or pale brown, sympodially proliferating, producing several cylindrical denticles in the apical region, (5–)7–17.5(–19) × 2.5–3 µm (av. ± SD = 12.4 ± 3.9 × 2.6 ± 0.3 µm, n = 30). *Conidia* solitary, medianly 1-septate, subcylindrical, apex obtuse, frills remaining on denticle and on conidial hilum, 0.5 µm long, medium brown, verruculose, released by rhexolytic secession, 8–11.5(–12) × 2.5–3.5 µm (av. ± SD = 9.6 ± 1.1 × 2.7 ± 0.3 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 24–26 mm diam after 14 d at 26 °C, brown, slightly raised in the centre, with moderate aerial mycelium and smooth. On OA reaching up to 20–22 mm diam, flat, spreading, dark brown. On MEA reaching 21–22 mm diam, raised, with moderate aerial mycelium, olivaceous.

Notes — *Scolecobasidium coiledmyces* is phylogenetically related to *S. cordanae* and *S. ailanthi*, but *S. coiledmyces* forms a single branch as the sister clade to the other two species with high support from three independent algorithms (Fig. 2). Furthermore, *S. coiledmyces* is distinct based on its morphology. The conidia of *S. cordanae* are smaller (5–10 × 2.5–3.5 µm vs 8–12 × 2.5–3.5 µm), obovoidal to broadly fusoid and constricted at the median septum (Samerpitak et al. 2014); *S. ailanthic* differed from our strain in having fusoid, longitudinally striate and smaller conidia (9–10 × 2.4–2.6 µm vs 8–12 × 2.5–3.5 µm) with a thick septum, as well as unbranched conidiophores (Jayasiri et al. 2019).

Scolecobasidium echinulatum T.P. Wei & Y.L. Jiang, *sp. nov.* — MycoBank MB 842082; Fig. 7

Etymology. The epithet refers to the conidia with minutely echinulate cell walls.

Typus. China, Guizhou Province, Guiyang City, Huaxi Wetland Park, N26°43'92" E106°67'76", 1140 m a.s.l., isolated from soil, 16 Nov. 2018, *T.P. Wei* (holotype HGUP 18247, isotype CGMCC 3.20552, culture ex-type GUCC 18247).

Mycelium superficial or immersed, hyphae brown, smooth, thin-walled, septate, 1.5–3 µm wide. *Conidiophores* clearly differentiated, arising at right angles from creeping hyphae, branched, erect, straight or slightly flexuous, brown, smooth, septate, (12–)13.5–70(–87) × (2.5–)3–4 µm (av. ± SD = 29.7 ± 18.1 × 3.1 ± 0.3 µm, n = 30). *Conidiogenous cells* integrated, terminal or intercalary, elongate to cylindrical, with some scattered denticles in the apical region, pale brown, smooth, (4–)5–15(–20.5) × 2.5–4 µm (av. ± SD = 9.8 ± 3.9 × 3.1 ± 0.4 µm, n = 30). *Conidia* ellipsoidal to cylindrical, verruculose or minutely echinulate, dark brown to black, 1(–2)-septate, slightly narrower around the middle, frills remaining on denticle and on conidial hilum, released by rhexolytic secession, 8.5–10(–11.5) × 4–5 µm (av. ± SD = 9.5 ± 0.9 × 4.3 ± 0.3 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 13–18 mm diam after 14 d at 26 °C, spreading, dark olivaceous brown. On OA reaching up to 18–20 mm diam, colonies moderately expanding, immersed, flat, dark olivaceous brown. On MEA reaching 13–15 mm diam, olivaceous, raised, with moderate aerial mycelium.

Additional material examined. China, Guizhou Province, Qingzhen City, Red maple lake scenic area, N26°54'35" E106°38'74", 1272 m a.s.l., from soil, 07 Aug. 2020, *T.P. Wei* (HGUP 18248), living culture GUCC 18248 = CGMCC 3.20553.

Notes — The proposed new species, *S. echinulatum*, is phylogenetically related to *S. phaeophorum* and *S. crassihumicola*, but they can be distinguished by their morphological characteristics and DNA sequence data. *Scolecobasidium echinulatum* differs from *S. phaeophorum* as it has ellipsoidal to cylindrical, verruculose or minutely echinulate, dark brown to black and 1(–2)-septate conidia (the cylindrical to fusoid conidia of *S. phaeophorum* are smooth-walled, pale brown and 1-septate) (Samerpitak et al. 2015b); *S. crassihumicola* differs from *S. echinulatum* by having 1(–3)-septate, non-constricted, ovoid to cylindrical and larger conidia (7.5–13 × 4.2–5.5 µm vs 8.5–11.5 × 4–5 µm) (Matsushima 1971).

Scolecobasidium obovoideum T.P. Wei & Y.L. Jiang, *sp. nov.* — MycoBank MB 842083; Fig. 8

Etymology. The epithet refers to the obovoidal conidia.

Typus. China, Guizhou Province, Guiyang City, Tianhetan Tourist Holiday Resort, N26°43'95" E106°57'64", 1164 m a.s.l., isolated from forest litter, 16 Dec. 2019, *T.P. Wei* (holotype HGUP 18246, isotype CGMCC 3.20551, culture ex-type GUCC 18246).

Mycelium composed of hyaline to pale brown, septate, branched, smooth, thick-walled, 1.5–3 µm wide hyphae. *Conidiophores* arising directly from vegetative hyphae, subcylindrical, branched, multi-septate, brown, erect, straight or flexuous, (7–)9.5–39.5(–43) × (2–)2.5–3.5 µm (av. ± SD = 20.0 ± 9.9 × 2.6 ± 0.4 µm, n = 30). *Conidiogenous cells* polyblastic, terminal or intercalary, subcylindrical to subclavate, pale brown, producing conidia sympodially on long open denticles, 6–14(–15.5) × 2–3.5 µm (av. ± SD = 9.4 ± 2.1 × 2.6 ± 0.4 µm, n = 30). *Conidia* solitary, obovoidal to fusoid, sometimes slightly apiculate at the base, finely verruculose, 1-septate, constricted at the septum, brown, released by rhexolytic secession, 5.5–8.5 × 2.5–4 µm (av. ± SD = 7.2 ± 0.6 × 3.1 ± 0.3 µm, n = 30).

Culture characteristics — Colonies on PDA reaching up to 19–20 mm diam after 14 d at 26 °C, with moderate aerial mycelium, dark brown. On OA reaching 24–26 mm diam, flat, immersed, olivaceous. On MEA reaching 19–21 mm diam, raised, aerial mycelium moderate to abundant, olive grey.

Notes — *Scolecobasidium obovoideum* is phylogenetically closely related to *S. pandanicola* and *S. dracaenae* and can be differentiated from that species by DNA sequences of ITS, LSU, SSU, *act1*, *tub2* and *tef1* gene regions. Morphologically, *S. pandanicola* can be distinguished from *S. obovoideum* as it has subhyaline to hazel brown, thin-walled, fusoid or ellipsoid

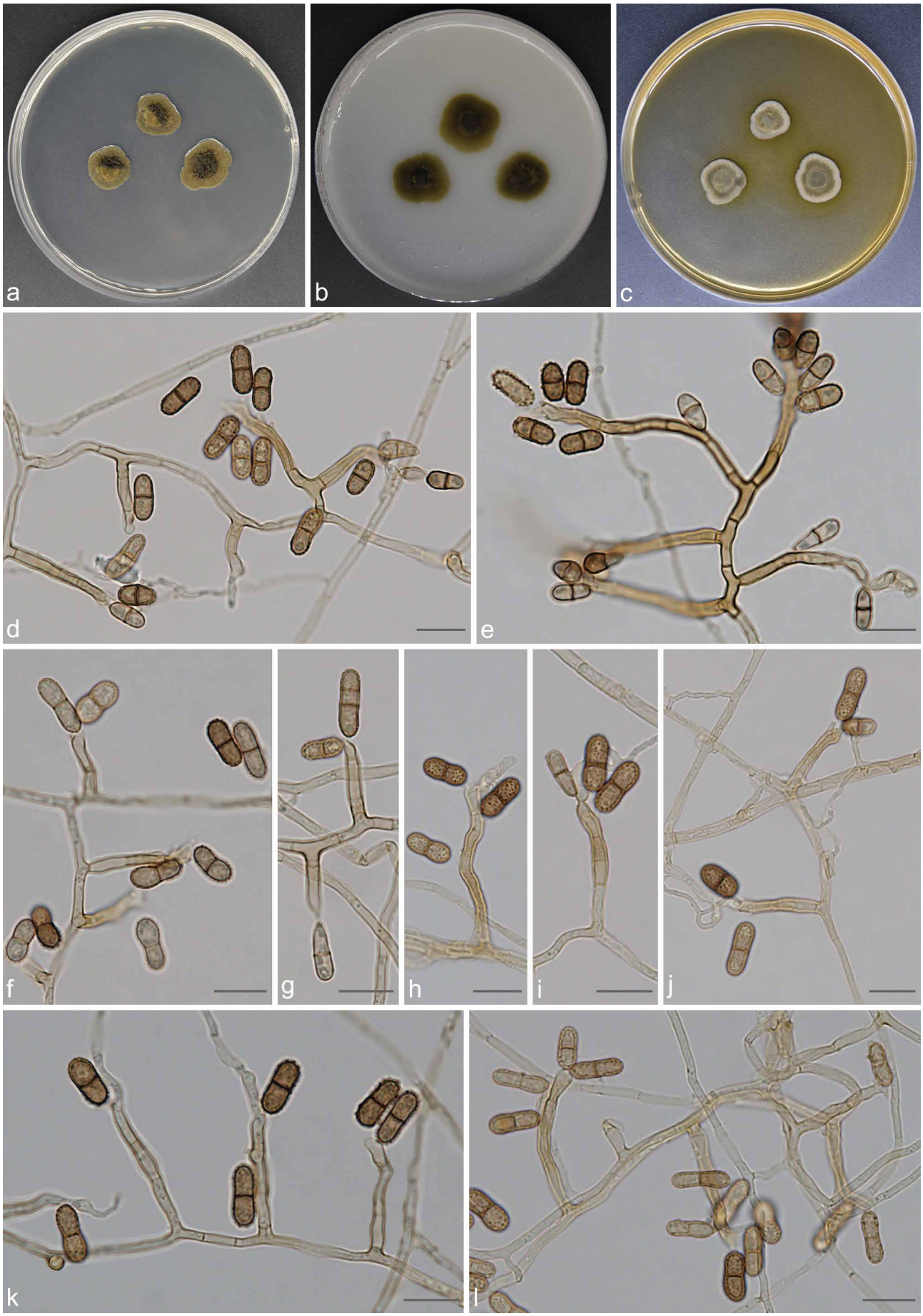

Fig. 7 *Scolecobasidium echinulatum* (culture ex-type GUCC 18247). a–c. Colony on PDA, OA and MEA; d–f. conidial apparatus with rhexolytic conidia, produced from sympodial conidiogenous cells; g. immature and 1(–2) septate conidia; h–l. conidiophores with conidiogenous cells and conidia. — Scale bars: d–l = 10 µm.

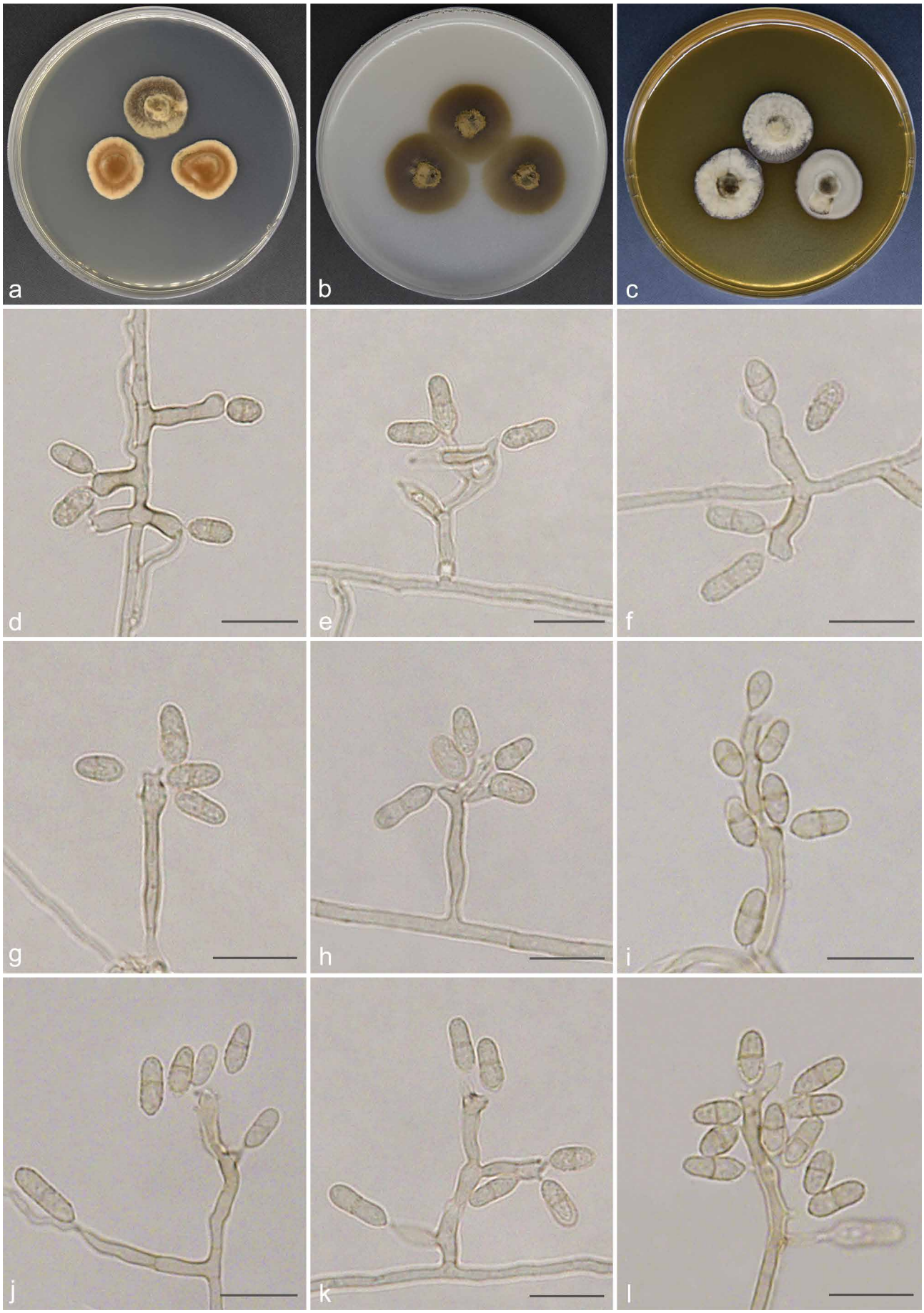

Fig. 8 *Scolecobasidium obovoideum* (culture ex-type GUCC 18246). a–c. Colony on PDA, OA and MEA; d–i. conidial apparatus with rhexolytic conidia, produced from sympodial conidiogenous cells; j–k. branched conidiophores; l. conidiophores with conidiogenous cells and conidia. — Scale bars: d–l = 10 µm.

Fig. 9 *Scolecobasidium verrucaria* (culture ex-type GUCC 18240). a–c. Colony on PDA, OA and MEA; d–f. conidiophores with conidiogenous cells and conidia; g. 1(–2) septate and coarsely verrucose conidia; h–p. maturation process of conidia. — Scale bars: d–p = 10 µm.

and larger conidia (6–10 × 3–4.5 µm vs 5.5–8.5 × 2.5–4 µm) (Crous et al. 2015); *S. dracaenae* differs from *S. obovoideum* in having subcylindrical and larger conidia (6.5–10 × 3–4 µm vs 5.5–8.5 × 2.5–4 µm), and shorter conidiophores (10–30 × 2–3 µm vs 7–43 × 2–3.5 µm) (Crous et al. 2016). Phylogenetically, our new isolate GUCC 18246 forms a single clade separated from other *Scolecobasidium* species (Fig. 2).

Scolecobasidium verrucaria T.P. Wei & Y.L. Jiang, *sp. nov.* — MycoBank MB 840924; Fig. 9

Etymology. The epithet refers to its verrucose conidia.

Typus. China, Guizhou Province, Qingzhen City, Red maple lake scenic area, N26°54'35" E106°38'74", 1272 m a.s.l., from soil, 16 Apr. 2018, *T.P. Wei* (holotype HGUP 18240, isotype CGMCC 3.20545, culture ex-type GUCC 18240).

Mycelium mostly superficial or semi-immersed, hyphae pale brown, smooth, branched, 1–2 µm wide. *Conidiophores* arising directly from vegetative hyphae, occasionally branched, continuous or septate, dark brown, straight or slightly geniculate, cylindrical, (12.5–)14.5–51.5(–54) × 3–3.5 µm (av. ± SD = 30.1 ± 11.8 × 2.9 ± 0.2 µm, n = 30). *Conidiogenous cells* integrated, terminal, polyblastic, sympodial, cylindrical, subhyaline, (6.5–)7–16.5(–17.5) × 2.5–3.5 µm (av. ± SD = 10.2 ± 2.8 × 2.7 ± 0.3 µm, n = 30), with one or more denticles in the apical region, denticles 1–3 µm long. *Conidia* acropleurogenous, broadly ellipsoidal, 1(–2)-septate, strongly constricted at the septum, 8.5–11(–11.5) × 4.5–5.5(–6) µm (av. ± SD = 9.3 ± 0.8 × 5.0 ± 0.3 µm, n = 30), the colour of immature conidia changed from brown to yellow to dark brown, and gradually from smooth to coarsely verrucose, verrucous protrusions up to 2.7 µm long.

Culture characteristics — Colonies on PDA reaching up to 20–22 mm diam after 14 d at 26 °C, slightly raised at centre, isabelline, lobate margin. On OA reaching 24–26 mm diam, flat, spreading, immersed, olivaceous. On MEA reaching 16–18 mm diam, raised, hairy, grey brown.

Notes — *Scolecobasidium verrucaria* was collected from natural forest soil, and has the same lifestyle as some species of *Scolecobasidium*. Morphologically, the polyblastic sympodial conidiogenous cells, conidial apparatus with rhexolytic conidiogenesis, and olivaceous colonies point to *Scolecobasidium*. It is noteworthy that the ellipsoidal, 1(–2)-septate, yellow to dark brown, and coarsely verrucose conidia of *S. verrucaria* differ from other reported members of *Scolecobasidium*. Phylogenetically, *S. verrucaria* nests in the *Scolecobasidium* clade, being closely related to *S. zunyiense*. However, *S. zunyiense* can be distinguished from *S. verrucaria* by its brown grey, verruculose, 0(–1)-septate and larger conidia (8.5–14 × 4–5.5 µm vs 8.5–11.5 × 4.5–6 µm).

Scolecobasidium zunyiense T.P. Wei & Y.L. Jiang, *sp. nov.* — MycoBank MB 840925; Fig. 10

Etymology. Named after Zunyi, where this species was collected.

Typus. China, Guizhou Province, Zunyi City, Phoenix Mountain National Forest Park, N27°36'27" E106°45'07", 1024 m a.s.l., from forest litter, 10 June 2019, *T.P. Wei* (holotype HGUP 18241, isotype CGMCC 3.20546, culture ex-type GUCC 18241).

Mycelium consisting of pale brown, smooth, branched, septate, 1.5–2.5 µm diam hyphae, often giving rise to hyphal coils. *Conidiophores* branched, straight to irregularly curved, solitary or at times two arising from the same basal cell, smooth, subcylindrical, septate, pale brown to brown, (9–)11–60(–78) × 3–4 µm (av. ± SD = 32.1 ± 15.9 × 3.2 ± 0.3 µm, n = 30). *Conidiogenous cells* polyblastic, sympodial, terminal or intercalary, subhyaline to brown, smooth, subcylindrical, (5–)5.5–15.5(–17.5) × 3–4 µm (av. ± SD = 9.8 ± 2.9 × 3.3 ± 0.3 µm, n = 30), with 1–9 terminal denticles, 1–2 µm. *Conidia* released by rhexolytic secession, solitary, acropleurogenous, ellipsoidal with rounded ends, 0(–1)-septate, brown grey, verruculose, prominently constricted at the septum, 8.5–13(–14) × 4–5.5 µm (av. ± SD = 10.2 ± 1.2 × 4.4 ± 0.4 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 18–20 mm diam after 14 d at 26 °C, slightly raised at centre, immersed, isabelline. On OA reaching up to 20–23 mm diam, flat, spreading, dark brown, reverse brown. On MEA reaching 20–22 mm diam, raised, hairy, pale brown at the surface, reverse olivaceous.

Notes — *Scolecobasidium zunyiense* is phylogenetically related to *S. verrucaria*, being fully supported in three independent algorithms (Fig. 2). Nevertheless, they can be distinguished based on their morphological characteristics as *S. zunyiense* is characterised by brown grey, 0(–1)-septate and verruculose conidia, while the conidia of *S. verrucaria* are yellow to dark brown, 1(–2)-septate, and verrucous protrusions can be up to 2.7 µm long, a feature not observed for *S. zunyiense*.

Scolecobasidium ferulica (Z. Tazik & K. Rahnama) T.P. Wei & Y.L. Jiang, *comb. nov.* — MycoBank MB 840930

Basionym. *Ochroconis ferulica* Z. Tazik & K. Rahnama, Nova Hedwigia 110: 374. 2020.

Description — Tazik et al. (2020).

Notes — *Scolecobasidium ferulica* was initially reported as an endophyte on roots of *Ferula ovina* in northeast Iran (Tazik et al. 2020). Multi-locus phylogenetic analyses indicate that this species is sister to *S. longiphorum* and is fully supported as phylogenetically distinct (Fig. 2). Morphologically, the ellipsoidal and smaller conidia of *S. ferulica* (8–10.5 × 6–7.5 µm) distinguishes this species from *S. longiphorum* (12–19 × 3.5–4.5 µm), which is characterised by long cylindrical and larger conidia (Samerpitak et al. 2014).

Scolecobasidium guangxiensis (Xie et al.) T.P. Wei & Y.L. Jiang, *comb. nov.* — MycoBank MB 840931

Basionym. *Ochroconis guangxiensis* Xie et al., Mycoscience 61: 308. 2020

Description — Chen et al. (2020).

Notes — *Scolecobasidium guangxiensis* was collected from rhizosphere soil of sugarcane in Guangxi, China, and was introduced by Chen et al. (2020). Based on the phylogeny presented here, despite the *S. guangxiensis* shares a sister relationship with *S. musicola* (Fig. 2), the considerably high number of variable positions in the ITS (88 bp, 17 %) and LSU (55 bp, 6 %) alignments supports the split into two distinct taxa. No SSU, *act1*, *tub2* and *tef1* data are currently available for the ex-type of *S. guangxiensis* and *S. musicola*. Morphologically, it is characterised by forming flask-shaped or cylindrical conidiophores and smooth-walled to verruculose, yellow brown, clavate or cylindrical, 1(–3)-septate conidia; *S. musicola* differs by its sexual morph forming fusoid to ellipsoid, hyaline to pale brown and straight to slightly curved ascospores (Crous et al. 2018b), whereas *S. guangxiensis* lacks a sexual morph.

Scolecobasidium helicteris (Singh et al.) T.P. Wei & Y.L. Jiang, *comb. nov.* — MycoBank MB 840932

Basionym. *Ochroconis helicteris* Singh et al., Phytotaxa 427: 192. 2019.

Description — Singh et al. (2019).

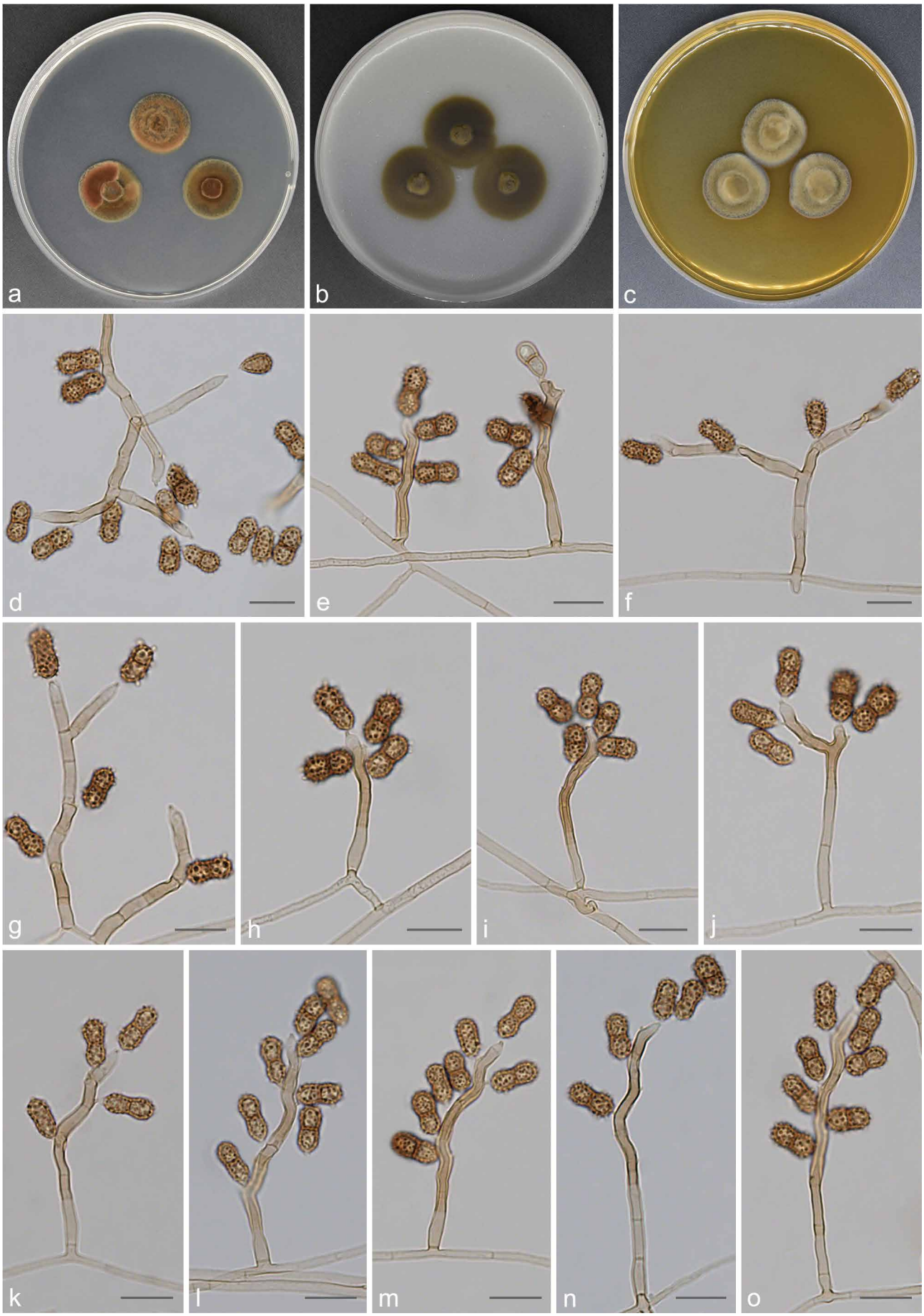

Fig. 10 *Scolecobasidium zunyiense* (culture ex-type GUCC 18241). a–c. Colony on PDA, OA and MEA; d–e. conidiophores and conidiogenous cells bearing conidia; f–g. branched conidiophores; h–o. acropleurogenous, ellipsoidal, 1-septate and verruculose conidia. — Scale bars: d–o = 10 µm.

Fig. 11 *Scolecobasidium leishanicola* (GUCC 18259). a–c. Colony on PDA, OA and MEA; d–e. conidial apparatus with rhexolytic conidia, produced from sympodial conidiogenous cells; f–l. germinating conidia; j–m. maturation process of conidia. — Scale bars: d–m = 10 µm.

Notes — *Scolecobasidium helicteris* was previously recorded as pathogen associated with leaf spots on *Helicteris isora* in India (Singh et al. 2019). According to our analysis, *S. helicteris* resolved as the closest phylogenetic relative to *S. ellipsoideum* (Fig. 2). *Scolecobasidium helicteris* is, however, clearly distinguished morphologically by its obovoid to fusoid or pear shaped and smooth to verruculose conidia, and shorter conidiophores (ellipsoidal to oblong and spinulose conidia in *S. ellipsoideum*) (Fig. 13; Ren et al. 2013).

Scolecobasidium leishanicola (X. Zhang & Y.L. Jiang) T.P. Wei & Y.L. Jiang, *comb. & nom. nov.* — MycoBank MB 840929; Fig. 11

Basionym. *Ochroconis terricola* X. Zhang & Y.L. Jiang, Mycotaxon 135: 146. 2020.

Mycelium consisting of branched, septate, subhyaline to pale brown, smooth-walled, 1.5–2.5 µm diam hyphae. *Conidiophores* arising directly from vegetative hyphae, erect, subcylindrical, unbranched, medium brown, multi-septate, smooth-walled, straight to flexuous, (9.5–)11–41(–108) × 2.5–4 µm (av. ± SD = 26.1 ± 18.6 × 3.2 ± 0.4 µm, n = 30). *Conidiogenous cells* integrated, terminal, subcylindrical, subhyaline to pale brown, with one to several sympodial denticle-like loci, (7.5–)9–23.5(–25) × (2.5–)3–4 µm (av. ± SD = 13.4 ± 4.6 × 3.1 ± 0.3 µm, n = 30). *Conidia* solitary, brown, ellipsoidal to cylindrical or fusoid, 1-septate, minutely echinulate, sometimes slightly constricted at the septum, apex obtuse, base narrowly truncated with hilum bearing a marginal frill, 9.5–12(–13.5) × 3–4.5 µm (av. ± SD = 11.6 ± 1.5 × 3.5 ± 0.4 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 22–24 mm diam after 14 d at 26 °C, effuse, grey brown, reverse dark brown, growing slowly. On OA reaching up to 24–26 mm diam, olivaceous brown, immersed, with sparse aerial mycelium. On MEA reaching 18–23 mm diam, spreading, hairy, isabelline, raised in the centre.

Material examined. China, Guizhou Province, Leishan County, N26°24'02" E107°77'22", 1178 m a.s.l., isolated from soil, 12 Mar. 2018, *T.P. Wei* (HGUP 18259), living culture GUCC 18259 = CGMCC 3.20564.

Notes — *Scolecobasidium leishanicola* (as *Ochroconis terricola*) was previously recorded from soil in China (Zhang et al. 2020). The phylogenetic tree constructed based on six gene loci showed that one isolate (GUCC 18259) from the present study clusters in a clade closely related to *S. leishanicola*, and was sister to *S. sexualis* and *S. podocarpicola* (Fig. 2). Morphologically, the conidial dimensions in the present study fit exactly with those in Zhang et al. (2020). Therefore, this species was placed in *Scolecobasidium*, for which a new name had to be introduced (*S. leishanicola*), as *S. terricola* was already occupied.

Scolecobasidium mirabilis (Samerp. & de Hoog) T.P. Wei & Y.L. Jiang, *comb. nov.* — MycoBank MB 840933

Basionym. *Ochroconis mirabilis* Samerp. & de Hoog, Fungal Diversity 65: 114. 2014.

Description — Samerpitak et al. (2014).

Notes — *Scolecobasidium musae* was originally isolated from the fruit surface of *Musa basjoo* in Hainan, China (Hao et al. 2013). Almost simultaneously, Samerpitak et al. (2014) described *S. mirabilis* from the regulator of a scuba diver in the Netherlands. Later, Samerpitak et al. (2015a) compared DNA sequence data between the two species and thought that the LSU sequences of *S. mirabilis* and *S. musae* were almost identical. To solve this taxonomic dilemma, they proposed *S. mirabilis* as a synonym for *S. musae*. However, our phylogenetic analysis indicates that *S. mirabilis* and *S. musae* cluster apart, and are phylogenetically distant (Fig. 2). They are genetically distinct in 2 bp (1 %), 21 bp (3 %), 3 bp (1 %), 10 bp (4 %), 46 bp (10 %) and 16 bp (4 %) in SSU, ITS, LSU, *act1*, *tub2* and *tef1* loci. Based on these results as well as their morphology, we thus resurrect *S. mirabilis* and recognise *S. mirabilis* and *S. musae* as two different species of *Scolecobasidium*.

Scolecobasidium constrictum E.V. Abbott, Mycologia 19: 30. 1927 — Fig. 12

Synonym. *Ochroconis constricta* (E.V. Abbott) de Hoog & Arx, Kavaka 1: 57. 1973.

Mycelium composed of hyaline or pale brown, septate, branched, smooth-walled, 1.5–2 µm diam hyphae. *Conidiophores* differentiated arising directly from vegetative hyphae, branched, sparingly septate, brown, smooth and thick-walled, cylindrical, mostly geniculate-sinuous, (11–)12–46.5(–56) × (2–)2.5–3.5 µm (av. ± SD = 23.8 ± 10.3 × 2.5 ± 0.3 µm, n = 30). *Conidiogenous cells* integrated, terminal, flask-shaped or ampulliform to cylindrical, hyaline or pale brown, with single or several sympodial apical loci with rhexolytic conidiogenesis, (3.5–)5.5–14(–15) × (2–)2.5–4(–4.5) µm (av. ± SD = 8.8 ± 3.1 × 3.0 ± 0.5 µm, n = 30). *Conidia* solitary, subhyaline to pale brown, 1-septate, broadly ellipsoidal to cylindrical, finely echinulate to verruculose, usually constricted at the septum, frills remaining on denticle and on conidial base, ends obtusely rounded, 9.5–12 × 3.5–4.5 µm (av. ± SD = 10.3 ± 0.6 × 3.9 ± 0.3 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 14–15 mm diam after 14 d at 26 °C, effuse, hairy, olivaceous brown, raised, usually slow-growing. On OA reaching up to 18–20 mm diam, cottony to floccose at centre, glabrous at periphery, grey olivaceous. On MEA reaching 14–15 mm diam, aerial mycelium moderate, olivaceous black, raised in the centre.

Materials examined. China, Guizhou Province, Shibing County, Fodingshan National Nature Reserve, N27°06'47" E108°10'82", 1180 m a.s.l., from dead branches, 12 Sept. 2020, *T.P. Wei* (HGUP 18255), living culture GUCC 18255 = CGMCC 3.20560; Guiyang City, Huaxi District, N26°42'55" E106°68'07", 1140 m a.s.l., from forest litter, 6 May 2018, *T.P. Wei* (HGUP 18256), living culture GUCC 18256 = CGMCC 3.20561; Qingzhen City, N26°54'35" E106°38'74", 1272 m a.s.l., from soil, 16 Apr. 2018, *T.P. Wei* (HGUP 18257), living culture GUCC 18257 = CGMCC 3.20562; Guiyang City, Guanshan Lake Park, N26°64'28" E106°63'06", 1260 m a.s.l., from lawn soil, 5 Apr. 2021, *T.P. Wei* (HGUP 18258), living culture GUCC 18258 = CGMCC 3.20563.

Notes — *Scolecobasidium constrictum* was reported by Abbott (1927) as the type species of *Scolecobasidium*, which is characterised by having ampulliform or cylindrical conidiogenous cells and broadly ellipsoidal to cylindrical conidia. The phylogenetic result shows that our four isolates cluster together with *S. constrictum* and are well-supported (Fig. 2). Therefore, we identified our isolates as *S. constrictum* and provide an illustration of the species.

Scolecobasidium ellipsoideum Ren et al., Mycoscience 54: 422. 2013 — Fig. 13

Mycelium partly superficial or semi-immersed, hyphae simple branched, septate, pale brown, smooth-walled, 1.5–2 µm wide. *Conidiophores* erect, branched, slightly to distinctly geniculate-sinuous, cylindrical, multi-septate, brown, smooth, (10.5–)11–64.5(–77.5) × (2–)2.5–3.5 µm (av. ± SD = 30.6 ± 19.7 × 2.6 ± 0.3 µm, n = 30). *Conidiogenous cells* terminal or intercalary, subcylindrical, pale to medium brown, producing conidia sympodially on long open denticles, (4–)6–10(–11) × 2–2.5(–3) µm (av. ± SD = 8.2 ± 2.2 × 2.3 ± 0.2 µm, n = 30). *Conidia* solitary, ellipsoidal to oblong, 1-septate, pale to dark brown, spinulose, apex

Fig. 12 *Scolecobasidium constrictum* (GUCC 18256). a–c. Colony on PDA, OA and MEA; d–m. conidial apparatus with rhexolytic conidia, produced from sympodial conidiogenous cells; n–o. hyphal coil; p. cylindrical to fusoid conidia. — Scale bars: d–p = 10 µm.

Fig. 13 *Scolecobasidium ellipsoideum* (GUCC 18264). a–c. Colony on PDA, OA and MEA; d–f. conidiophores and conidiogenous cells bearing conidia; g. branched conidiophores; h–p. medium brown, 1-septate and ellipsoidal to cylindrical conidia. — Scale bars: d–p = 10 µm.

Fig. 14 *Scolecobasidium globale* (GUCC 18249). a–c. Colony on PDA, OA and MEA; d–k. hyphae, conidiophores with sympodially proliferating conidiogenous cells and cylindrical to pyriform and rhexolytic succession conidia; l. germinating conidia. — Scale bars: d–l = 10 µm.

subobtuse, base truncate with basal marginal frill, sometimes slightly constricted at the septum, released by rhexolytic secession, 7.5–9.5 × 3–4 µm (av. ± SD = 8.2 ± 0.7 × 3.3 ± 0.3 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 17–25 mm diam after 14 d at 26 °C, spreading, yellow brown, with moderate aerial mycelium. On OA reaching up to 26–32 mm diam, immersed, olivaceous, with sparse aerial mycelium. On MEA reaching 20–24 mm diam, raised in the centre, grey olivaceous.

Materials examined. China, Guizhou Province, Leishan County, N26°24'02" E107°77'22", 1178 m a.s.l., from soil, 12 Mar. 2018, *X. Zhang* (HGUP 18264), living culture GUCC 18264 = CGMCC 3.20569; Meitan County, N27°75'09" E107°47'99", 910 m a.s.l., from submerged wood, 10 Aug. 2019, *T.P. Wei* (HGUP 18265), living culture GUCC 18265 = CGMCC 3.20570; Zunyi City, N27°36'27" E106°45'07", 1024 m a.s.l., from forest litter, 10 June 2019, *T.P. Wei* (HGUP 18266), living culture GUCC 18266 = CGMCC 3.20571.

Notes — *Scolecobasidium ellipsoideum* was originally described as a saprophyte from soils in Guizhou Province, China (Ren et al. 2013). In this study, phylogenetic inference revealed that our three newly collected isolates clustered together with the ex-type strains of *S. ellipsoideum* (Fig. 2). The morphological characters of our studied specimens fit well with *S. ellipsoideum* (Fig. 13). Moreover, *S. ellipsoideum* differs from the phylogenetically related species *S. helicteris* by nucleotide differences in ITS (7 bp, 1 %) and *tub2* (GUCC 18264: 3 bp, 2 %). No LSU, SSU, *act1* and *tef1* are available for the ex-type of *S. ellipsoideum* and *S. helicteris*.

Scolecobasidium globale (Samerpitak et al.) Crous et al., Stud. Mycol. 96: 211. 2020 — Fig. 14

Basionym. *Ochroconis globalis* Samerpitak et al., Mycol. Progr. 14: 3. 2015.

Mycelium superficial or immersed, hyphae septate, hyaline to pale brown, smooth and thin-walled, 1.5–2 µm wide. *Conidiophores* differentiated arising directly from vegetative hyphae, straight to flexuous, cylindrical, multi-septate, branched, pale to dark brown, (20.5–)27.5–190(–211.5) × (2.5–)3–4.5(–5.5) µm (av. ± SD = 99.7 ± 59.8 × 3.7 ± 0.8 µm, n = 30). *Conidiogenous cells* terminal or intercalary, proliferating sympodially, with a single or more denticle-like conidiogenous loci, subhyaline to brown, (6.5–)7.5–22(–30.5) × 3.5–4.5(–5) µm (av. ± SD = 12.7 ± 6.8 × 3.7 ± 0.4 µm, n = 30). *Conidia* solitary, ellipsoidal to cylindrical, brown, 1(–3)-septate, smooth or somewhat verrucose, constricted at the septum, frills remaining visible on denticle and on conidial base, (7–)8.5–10(–11.5) × 4–5.5(–6) µm (av. ± SD = 9.7 ± 1.6 × 5.1 ± 0.7 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 10–11 mm diam after 14 d at 26 °C, surface yellow brown, growing slowly, with sparse aerial mycelium. On OA reaching up to 13–16 mm diam, moderately expanding, immersed, olivaceous. On MEA reaching 12–13 mm diam, raised, hairy, brownish olive green.

Materials examined. China, Guizhou Province, Shiqian County, Ganxi Township, Fodingshan National Nature Reserve, N27°40'51" E108°07'21", 1240 m a.s.l., from forest humus, 2 Nov. 2019, *T.P. Wei* (HGUP 18249), living culture GUCC 18249 = CGMCC 3.20554; Guiyang City, Tianhetan Tourist Holiday Resort, N26°43'95" E106°57'64", 1164 m a.s.l., from soil, 26 Oct. 2020, *T.P. Wei* (HGUP 18250), living culture GUCC 18250 = CGMCC 3.20555.

Notes — *Scolecobasidium globale* was introduced by Samerpitak et al. (2015a). In this study, two newly collected isolates clustered together with *S. globale* and were fully supported phylogenetically (Fig. 2). The comparison of morphological characteristics of the three strains found them to be similar. However, our newly obtained isolates differ from the ex-type culture of *S. globale* in having more septate conidia (mostly 1-septate in CBS 119644 vs up to 1(–3)-septate in GUCC 18249) (Samerpitak et al. 2015a; Fig. 14), which may depend on the state (mature or immature) of the specimen being observed. Importantly, the ex-type culture (CBS 119644) of *S. globale* had the following nucleotide similarities with the sequences of our newly collected strain (GUCC 18249). On ITS, LSU, SSU, *act1*, *tub2* and *tef1*, respectively: 677/687 (99 %, including six gaps), 791/794 (99 %, including two gaps), 1463/1464 (99 %, including one gap), 334/348 (96 %, including 12 gaps), 459/488 (94 %, including seven gaps) and 508/513 (99 %, including one gap). Therefore, we identified our isolates as *S. globale*, and provide an illustration from a different host, representing a new record from China.

Scolecobasidium minimum (Fassat.) Crous et al., Stud. Mycol. 96: 212. 2020 — Fig. 15

Basionym. *Humicola minima* Fassat., Ceská Mykol. 21: 87. 1967.

Synonym. *Ochroconis minima* (Fassat.) Samerpitak & de Hoog, Fungal Diversity 65: 110. 2013.

Mycelium consisting of hyaline to yellow brown, smooth, septate, branched, 1.5–2.5 µm diam hyphae. *Conidiophores* hyaline to brown, cylindrical, septate, straight to flexuous, branched, mostly reduced to conidiogenous cells, 7–29(–36.5) × 2.5–4 µm (av. ± SD = 14.6 ± 8.4 × 3.1 ± 0.5 µm, n = 30). *Conidiogenous cells* flask-shaped to clavate, pale brown, mostly standing at right angles from undifferentiated hyphae, with some scattered denticles in the apical region, 5.5–11.5(–15) × 3–4 µm (av. ± SD = 8.6 ± 2.1 × 3.3 ± 0.4 µm, n = 30). *Conidia* acrogenous, yellow brown, 1-septate, smooth, somewhat T- or Y- shaped, composed of the main axis and two branches, branch form an angle of 45° with the apex of main axis; main axis 9–14.5 × 3–4 µm (av. ± SD = 10.9 ± 1.3 × 3.3 ± 0.2 µm, n = 30), secondary branches 1.5–5 × 2.5–4.5 µm (av. ± SD = 3.4 ± 0.7 × 3.6 ± 0.3 µm, n = 30). *Chlamydospores* spherical, dark brown, aseptate, smooth, arising directly from vegetative hyphae, 5–6 µm (av. ± SD = 5.4 ± 0.2, n = 30).

Culture characteristics — Colonies on PDA attaining 17–21 mm diam after 14 d at 26 °C, dark brown at centre, pale yellowish at periphery, fluffy aerial mycelium. On OA reaching up to 20–23 mm diam, pale olivaceous brown, with sparse aerial mycelium. On MEA reaching 19–21 mm diam, raised, centre olivaceous to grey olivaceous and white toward the periphery.

Material examined. China, Guizhou Province, Shiqian County, Fodingshan National Nature Reserve, N27°40'49" E108°07'35", 1100 m a.s.l., from forest humus, 2 Nov. 2019, *T.P. Wei* (HGUP 18260), living culture GUCC 18260 = CGMCC 3.20565.

Notes — In the current study, the phylogenetic result shows that our new collection GUCC 18260 clusters together with *S. minimum*, sharing a sister relationship to *S. ramosum* and *S. icarus* with high statistical support from three independent algorithms (Fig. 2). All three species have T- or Y-shaped conidia. Chen et al. (2020) obtained *S. minimum* from sugarcane and banana rhizospheres in Guangxi. Therefore, this is the second report of this species from China.

Scolecobasidium ramosum (Giraldo et al.) Crous et al., Stud. Mycol. 96: 212. 2020 — Fig. 16

Basionym. *Ochroconis ramosa* Giraldo et al., J. Clinical Microbiol. 52: 4197. 2014.

Mycelium composed of branched, septate, hyaline to pale brown, smooth-walled, 1.5–2 µm diam hyphae. *Conidiophores* pale brown, clavate or cylindrical with beaked apex, simple or sympodially branched, often reduced to conidiogenous cells, 7.5–64 (–69.5) × 3–4 µm (av. ± SD = 21.2 ± 14.6 × 3.1 ± 0.3 µm, n = 30).

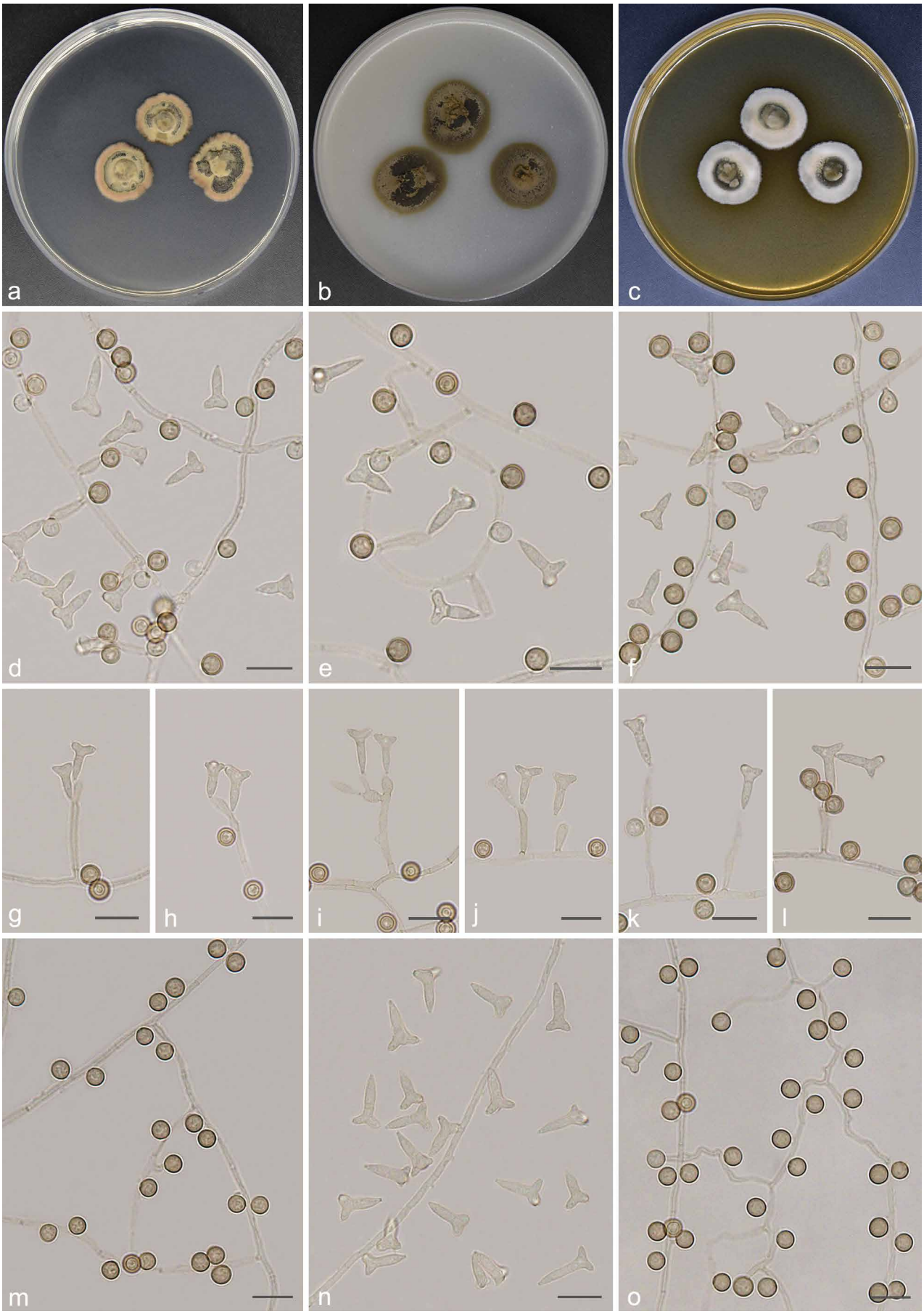

Fig. 15 *Scolecobasidium minimum* (GUCC 18260). a–c. Colony on PDA, OA and MEA; d–l. conidial apparatus with rhexolytic conidia, produced from sympodial conidiogenous cells; n. T- or Y- shaped conidia; m, o. chlamydospores. — Scale bars: d–o = 10 µm.

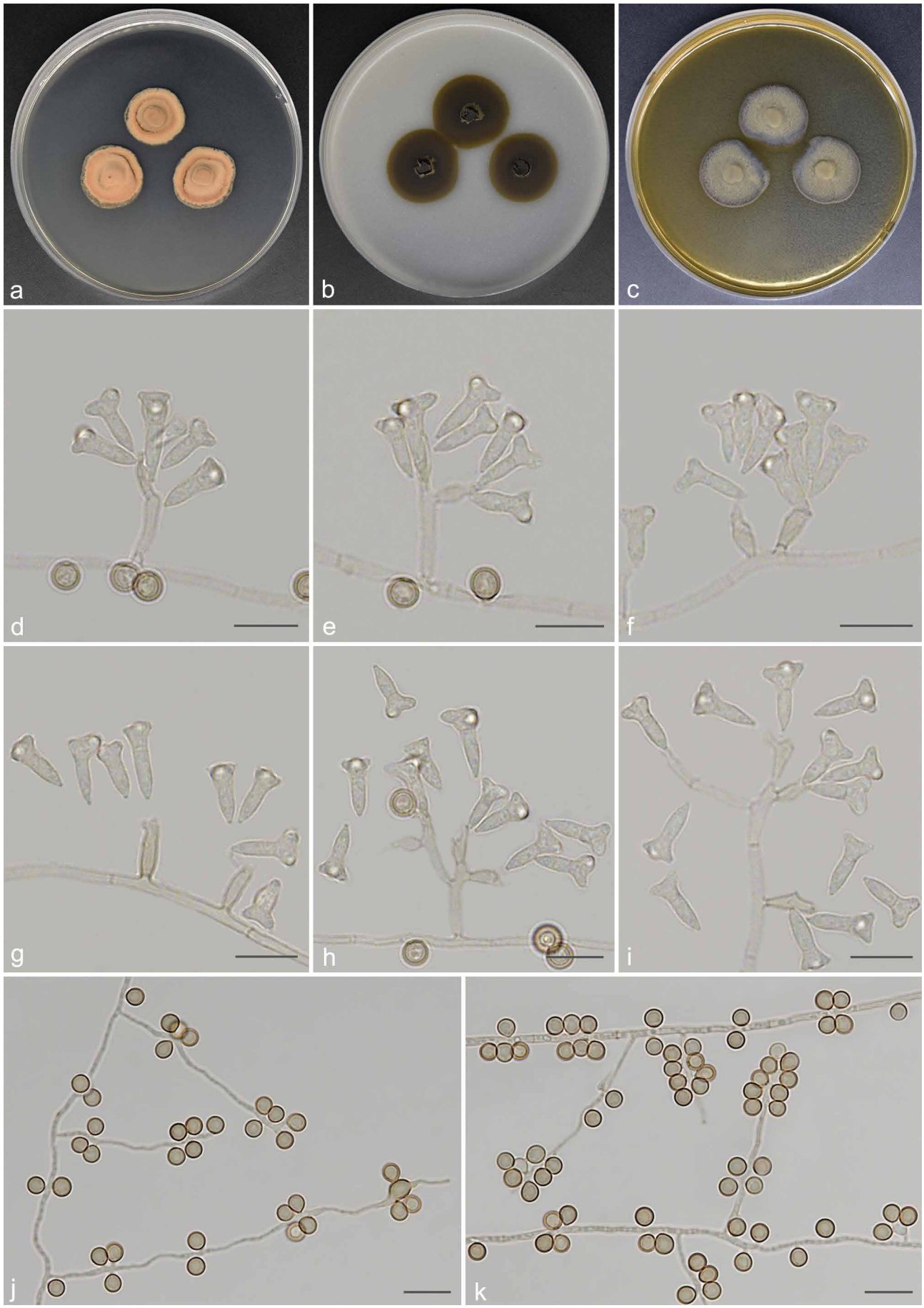

Fig. 16 *Scolecobasidium ramosum* (GUCC 18261). a–c. Colony on PDA, OA and MEA; d–i. hyphae, conidiophores with sympodially proliferating conidiogenous cells and T- or Y- shaped and rhexolytic succession conidia; j–k. chlamydospores. — Scale bars: d–k = 10 µm.

Conidiogenous cells subhyaline to pale brown, bearing one or more denticles in the apical region, ampulliform to cylindrical, 5.5–14.5(–17.5) × 2.5–4 µm (av. ± SD = 9.1 ± 2.9 × 3.1 ± 0.4 µm, n = 30). *Conidia* solitary, pale brown, 1-septate, trilobate, T- or Y-shaped, smooth or verrucose, base slightly tapered to truncate hilum, main axis 10–13.5 × 3–4 µm (av. ± SD = 11.3 ± 0.9 × 3.5 ± 0.2 µm, n = 30), secondary branches 1.5–6.5 × 3–5.5 µm (av. ± SD = 3.5 ± 1.2 × 4 ± 0.4 µm, n = 30), released by rhexolytic secession. *Chlamydospores* solitary, growing directly on vegetative hyphae, globose or subglobose, aseptate, dark brown, sessile, smooth, 4.5–5.5 µm (av. ± SD = 4.5 ± 0.2 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 17–20 mm diam after 14 d at 26 °C, slightly raised, yellow-brown, spreading. On OA reaching up to 21–23 mm diam, flat, chocolate brown, felty at center, membranous toward the periphery. On MEA reaching 19–20 mm diam, olivaceous grey, velvety to cottony, slightly raised to umbonate.

Materials examined. China, Guizhou Province, Zunyi City, Phoenix Mountain National Forest Park, N27°36'27" E106°45'07", 1024 m a.s.l., from forest litter, 10 June 2019, *T.P. Wei* (HGUP 18261), living culture GUCC 18261 = CGMCC 3.20566; Qingzhen City, N26°54'35" E106°38'74", 1272 m a.s.l., from soil, 16 Apr. 2018, *T.P. Wei* (HGUP 18262), living culture GUCC 18262 = CGMCC 3.20567; Leishan County, N26°24'02" E107°77'22", 1178 m a.s.l., from forest litter, 12 Mar. 2018, *T.P. Wei* (HGUP 18263), living culture GUCC 18263 = CGMCC 3.20568.

Notes — *Scolecobasidium ramosum* is phylogenetically closely related to *S. minimum* and *S. icarus* (Fig. 2). The sequences of ITS, LSU, SSU, *act1*, *tub2* and *tef1* gene regions can differentiate *S. ramosum* from these two species. This species was originally collected from human nails in the USA (Giraldo et al. 2014). Recently, Chen et al. (2020) isolated this species from the soil rhizosphere of sugarcane, and the strain we obtained was derived from forest litter and soil, which indicates that *S. ramosum* has both a parasitic and saprophytic lifestyle.

Scolecobasidium tshawytschae (Doty & D.W. Slater) McGinnis & Ajello, Trans. Brit. Mycol. Soc. 63: 202. 1974 — Fig. 17

Basionym. *Heterosporium tshawytschae* Doty & D.W. Slater, Amer. Midl. Naturalist 36: 663. 1946.

Synonym. *Ochroconis tshawytschae* (Doty & D.W. Slater) Kiril. & Al-Achmed, Mykrobiol. Zhurn. 39: 305. 1977.

Mycelium superficial or immersed, hyphae branched, septate, hyaline to pale brown, smooth and thin-walled, 1.5–2.5 µm wide. *Conidiophores* erect, cylindrical, straight to gently curved, septate, unbranched, mostly reduced to conidiogenous cells, (5.5–)6.5–18.5(–24) × 3–3.5(–4) µm (av. ± SD = 11.6 ± 5.1 × 3.2 ± 0.3 µm, n = 30). *Conidiogenous cells* integrated, terminal, often somewhat inflated, lageniform or ampulliform, with one to several conidiogenous loci, leaving minute collarettes on denticulate loci, 5–7.5(–9) × 4–5 µm (av. ± SD = 6.5 ± 1.1 × 4.1 ± 0.4 µm, n = 30). *Conidia* solitary, verrucose, pale to dark brown, 1(–3)-septate, cylindrical or slightly clavate, the colour of immature conidia changed from greenish olivaceous to yellow to dark brown, 12.5–22(–24.5) × (4.5–)5–6(–6.5) µm (av. ± SD = 16.4 ± 1.6 × 5.2 ± 0.4 µm, n = 30). *Chlamydospores* acrogenous, brown, smooth, 0(–1)-septate, ellipsoidal to fusoid, arising directly from vegetative hyphae, 7.5–13 × (4–)4.5–6(–6.5) µm (av. ± SD = 9.7 ± 1.9 × 4.8 ± 0.6 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 15–18 mm diam after 14 d at 26 °C, olivaceous at centre, dark brown at periphery, slightly raised to umbonate. On OA reaching up to 20–22 mm diam, felty, olivaceous brown to olive, submerged mycelium. On MEA reaching 20–22 mm diam, slightly domed, woolly, with dense dark hairs at the centre and grey loose mycelium near the edge.

Materials examined. China, Guizhou Province, Guiyang City, Guanshan Lake Park, N26°64'28" E106°63'06", 1260 m a.s.l., from lawn soil, 5 Apr. 2021, *T.P. Wei* (HGUP 18251), living culture GUCC 18251 = CGMCC 3.20556; Zunyi City, N27°36'27" E106°45'07", 1024 m a.s.l., from plant litter, 10 June 2019, *T.P. Wei* (HGUP 18252), living culture GUCC 18252 = CGMCC 3.20557; Guiyang City, Huaxi District, N26°42'55" E106°68'07", 1140 m a.s.l., isolated from soil, 6 May 2018, *T.P. Wei* (HGUP 18253), living culture GUCC 18253 = CGMCC 3.20558; Shiqian County, Pingshan Township, N27°40'50" E108°07'30", 1100 m a.s.l., isolated from soil, 2 Nov. 2019, *T.P. Wei* (HGUP 18254), living culture GUCC 18254 = CGMCC 3.20559.

Notes — *Scolecobasidium tshawytschae* was originally isolated as the etiologic agent of kidney mycosis in chinook salmon (*Oncorhynchus tshawytscha*) smolts (Doty & Slater 1946). The four strains (GUCC 18251 to GUCC 18254) obtained in the present study and many strains that have been reported so far originate in soil and plant litter (Barron & Busch 1962, Hamayun et al. 2009, Samerpitak et al. 2014), indicating that this species can also be saprophytic, corroborating the supposition that its infective ability in fish is purely opportunistic.

Verruconis Samerpitak et al., Fungal Diversity 65: 117. 2013 '2014'

Type species. *Verruconis gallopava* (W.B. Cooke) Samerpitak & de Hoog.

Notes — *Verruconis* was established by Samerpitak et al. (2014) to accommodate thermophilic species separated from *Ochroconis* (*O. calidifluminalis* and *O. gallopava*) and *Scolecobasidium* (*S. verruculosum*), with the type species, *V. gallopava* being an opportunistic neurotropic pathogen (Salkin et al. 1990, Seyedmousavi et al. 2013, Wang et al. 2018, Samerpitak et al. 2019). Therefore, thermophilicity and unbranched conidia were the main characteristics distinguishing this genus from *Ochroconis*. Subsequently, Zhang et al. (2018) and Qiao et al. (2019) successively placed the mesophilic species *V. panacis*, *V. hainanensis* and *V. pseudotricladiata* with Y- or T-shaped and cylindrical conidia under *Verruconis*. They found that *Verruconis* is not limited to thermophilic species with clavate to cylindrical conidia (Hernández-Restrepo et al. 2020). However, the addition of these species blurred the major distinguishing feature between *Verruconis* and *Ochroconis*. In contrast, the molecular systematics has played an important role in the taxonomy of these two genera (Machouart et al. 2014, Huanraluek et al. 2019, Shen et al. 2020). Samerpitak et al. (2016) revealed that the concatenated dataset of SSU, ITS, LSU, *act1*, *tub2* and *tef1* served as a reference for genus and species delimitations of *Ochroconis* and *Verruconis* (Lackner et al. 2014, Al-Hatmi et al. 2016). It is noteworthy that *V. mangrovei* is the first reported sexual species in *Verruconis* (Hyde et al. 2020).

Verruconis cylindricalis T.P. Wei & Y.L. Jiang, *sp. nov.* — MycoBank MB 840928; Fig. 18

Etymology. The epithet refers to its cylindrical chlamydospores.

Typus. China, Guizhou Province, Shiqian County, Fodingshan National Nature Reserve, N27°40'49" E108°07'35", 1100 m a.s.l., from forest humus, 2 Nov. 2019, *T.P. Wei* (holotype HGUP 18299, isotype CGMCC 3.20573, culture ex-type GUCC 18299).

Mycelium consisting of branched, subhyaline or pale brown, smooth, 1–3 µm thick hyphae, frequently forming hyphal coils. *Conidiophores* solitary, straight or flexuous, subcylindrical, pale brown, sparsely septate, (21–)27–57.5(–87.5) × 2.5–3(–3.5) µm (av. ± SD = 44.3 ± 22.2 × 2.6 ± 0.3 µm, n = 30). *Conidiogenous cells* integrated, terminal, sympodial, denticulate, bearing 1–2 conidium at the apex, (8–)9.5–16(–17.5) × 2.5–3(–3.5) µm (av. ± SD = 12.0 ± 3.6 × 2.5 ± 0.4 µm, n = 30). *Conidia* sparse on PDA and MEA, broadly ellipsoidal with prominent hila, 1-septate, minutely echinulate, brown to olivaceous brown, slightly constricted at the septum, (7–)7.5–12 × 4–5 µm

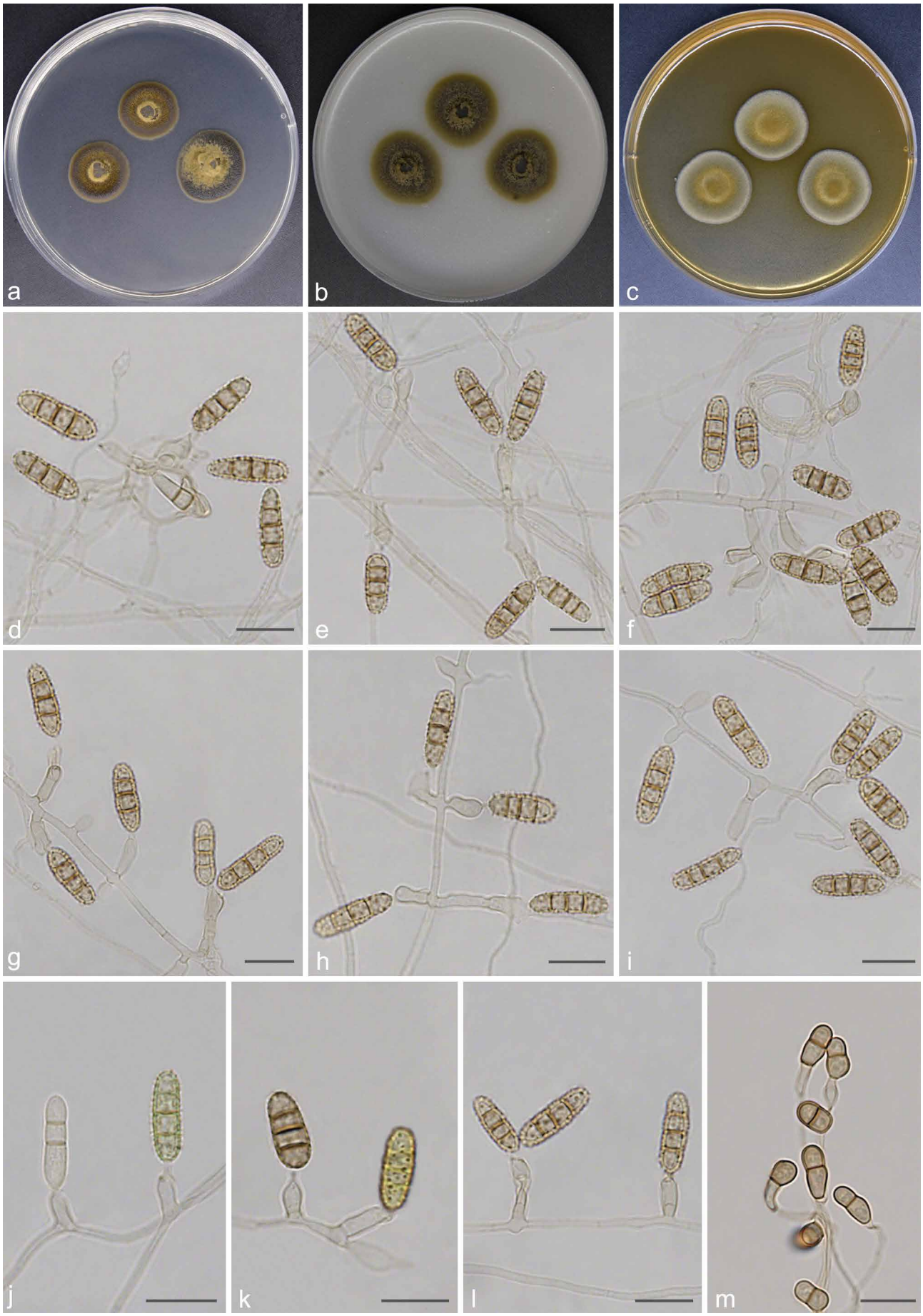

Fig. 17 *Scolecobasidium tshawytschae* (GUCC 18254). a–c. Colony on PDA, OA and MEA; d–h. conidial apparatus with rhexolytic conidia; i. conidiophores reduced to conidiogenous cells; j–l. maturation process of conidia; m. chlamydospores. — Scale bars: d–m = 10 µm.

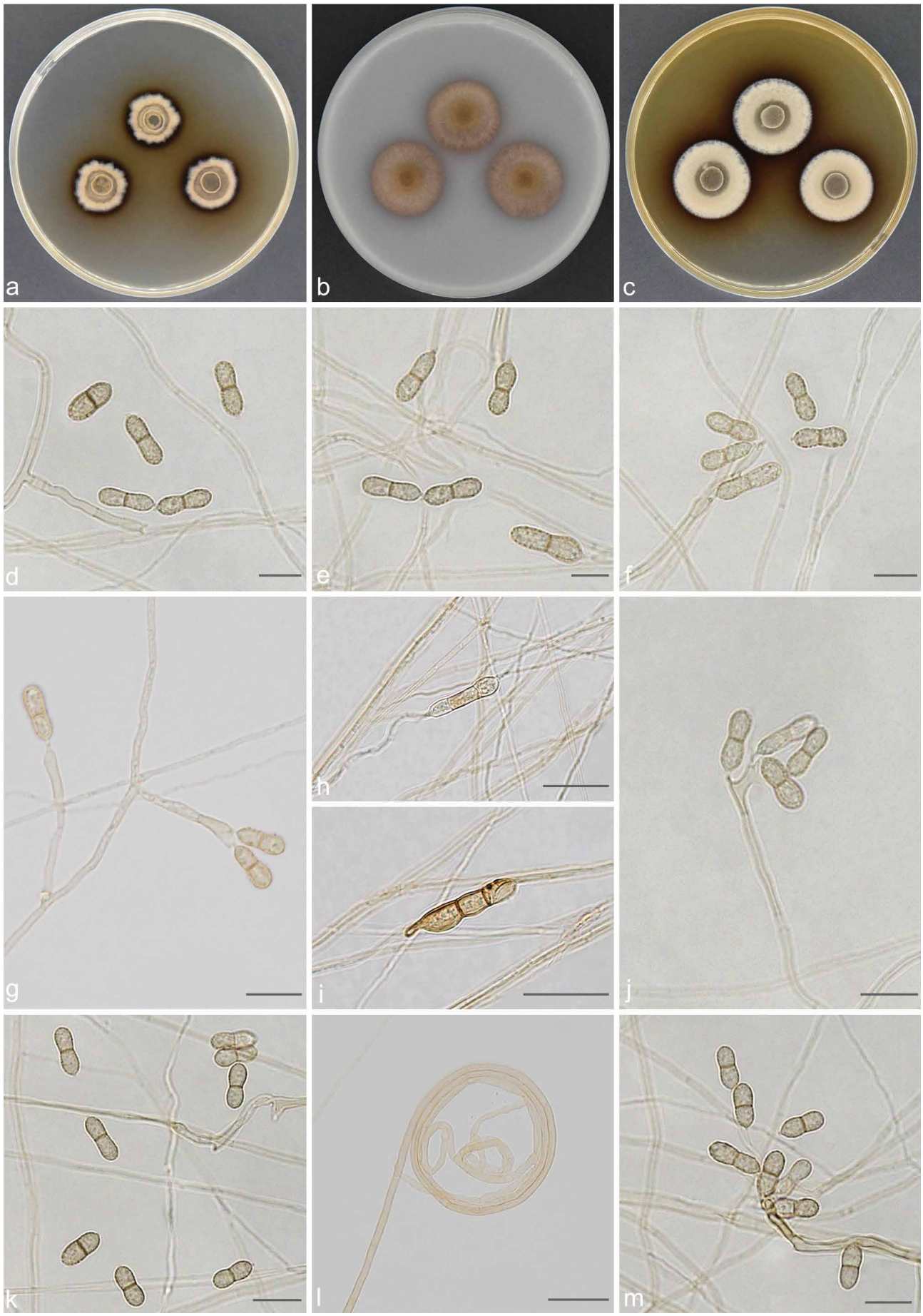

Fig. 18 *Verruconis cylindricalis* (culture ex-type GUCC 18299). a–c. Colony on PDA, OA and MEA; d–g, j–k, m. conidial apparatus with rhexolytic conidia, produced from sympodial conidiogenous cells; h–i. chlamydospores; l. hyphal coil. — Scale bars: h–i, l = 20 µm, all others = 10 µm.

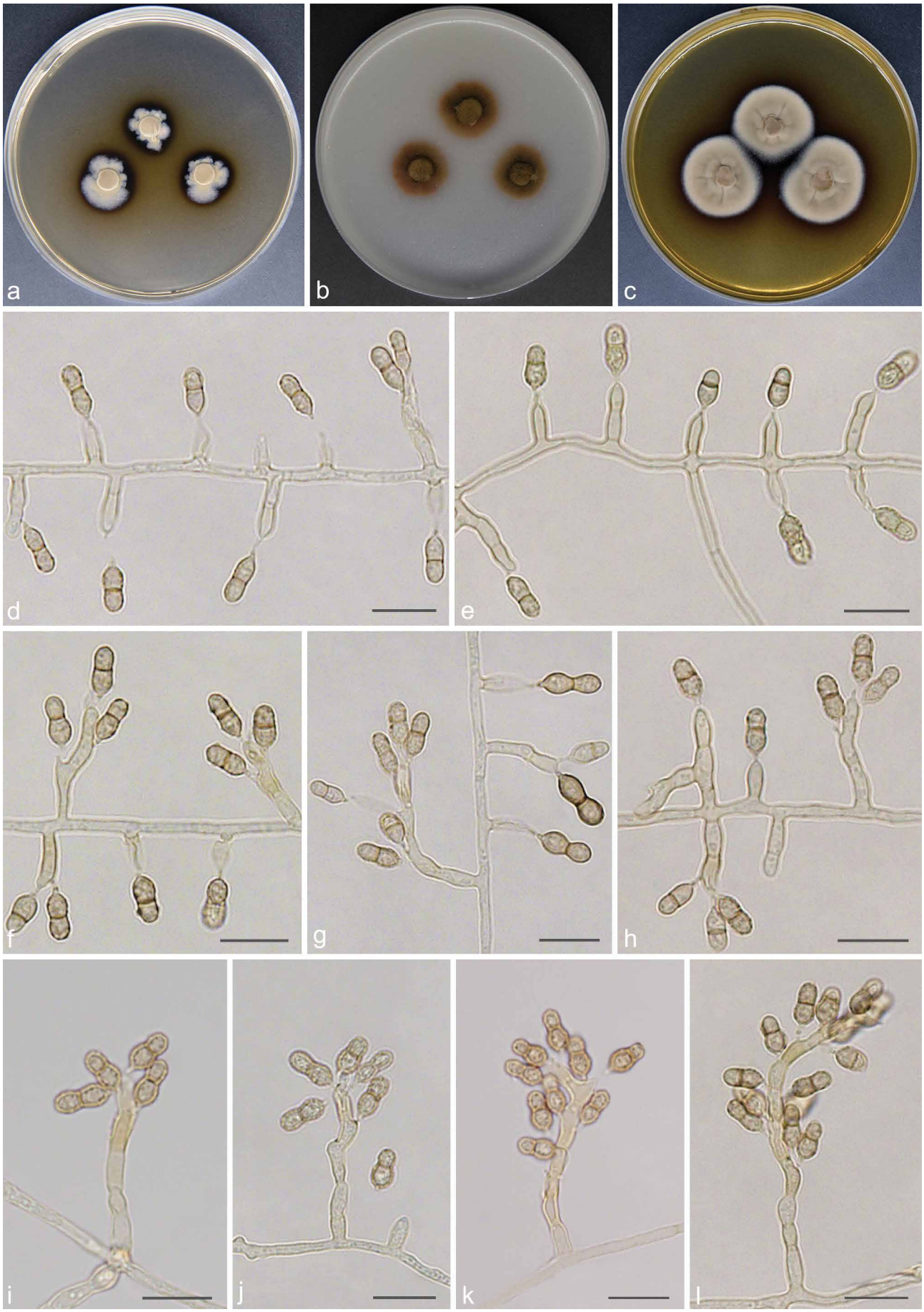

Fig. 19 *Verruconis thailandica* (GUCC 18267). a–c. Colony on PDA, OA and MEA; d–e. conidiophores reduced to conidiogenous cells; f–l. hyphae, conidiophores with sympodially proliferating conidiogenous cells and ellipsoidal and rhexolytic succession conidia. — Scale bars: d–l = 10 µm.

(av. ± SD = 9.4 ± 1.2 × 4.3 ± 0.2 µm, n = 30). *Chlamydospores* intercalary, verruculose, cylindrical or clavate, slightly tapered at both ends, 2-septate, often asymmetric with smaller middle cells, olivaceous brown, usually constricted at the septum, 25–29.5 × 4.5–6 µm (av. ± SD = 26.9 ± 2.2 × 5.1 ± 0.6 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 17–20 mm diam after 14 d at 26 °C, brown, margin irregular, submerged mycelium. On OA reaching up to 23–25 mm diam, velvety, dark brown, woolly at centre. On MEA reaching 20–23 mm diam, hairy, olivaceous brown. On PDA and MEA reverse blood colour with diffuse blood pigment spreading into agar.

Notes — *Verruconis cylindricalis* shares a few morphological similarities with *V. thailandica* and *V. calidifluminalis* in having two-celled conidia with protuberant hila. However, *V. thailandica* produces smaller, verrucose conidia (5–7 × 2.2–3.1 µm vs 7–12 × 4–5 µm), with a wing-like gelatinous brown sheath (Hernández-Restrepo et al. 2020). The conidia of the *V. calidifluminalis* are cylindrical to clavate, pale to dark brown and larger (9.5–20.5 × 2.5–5.0 µm vs 7–12 × 4–5 µm) (Yarita et al. 2010). Additionally, *V. cylindricalis* has longer conidiophores, cylindrical or clavate and 2-septate chlamydospores. These characters form the most notable differences with respect to *V. thailandica* and *V. calidifluminalis*. Phylogenetically, *V. cylindricalis* clustered in a distinct clade with full support from three independent algorithms (Fig. 2).

Verruconis tricladiata (Matsush.) T.P. Wei & Y.L. Jiang, *comb. nov*. — MycoBank MB 842456

Basionym. *Scolecobasidium tricladiatum* Matsush., Microfungi Solomon Isl. Papua-New Guinea: 52. 1971.

Description — Matsushima (1971).

Notes — *Scolecobasidium tricladiatum* was introduced based on its Y- or T-shaped or ellipsoidal to fusoid conidia, a species previously isolated from rotten leaves in Papua New Guinea (Matsushima 1971). Although we did not locate the type specimen, we have examined the DNA sequence data of another culture lodged under this species name in GenBank. Multi-locus phylogenetic analysis showed it to cluster in *Verruconis*, as sister to *V. pseudotricladiata* (Fig. 2). Nevertheless, *S. tricladiatum* and *V. pseudotricladiata* are genetically distinct in 6 bp (1 %), 87 bp (10 %) and 85 bp (9 %) in SSU, LSU and *tef1* loci. No ITS, *act1* and *tub2* data are currently available for *S. tricladiatum*. Morphologically, *S. tricladiatum* differs from *V. pseudotricladiata* by its moniliform, irregularly branched conidiophores and mostly unbranched, pale olivaceous to brown, verruculose conidia (Matsushima 1971, Qiao et al. 2019). Based on morphological characters and phylogenetic analyses, we therefore transferred *S. tricladiatum* to *Verruconis*.

Verruconis thailandica Giraldo López & Crous, Fung. Syst. Evol. 6: 21. 2020 — Fig. 19

Mycelium composed of branched, septate, pale brown, smooth, thin-walled, 2–2.5 µm diam hyphae. *Conidiophores* erect, arising directly from vegetative hyphae, sometimes reduced to conidiogenous cells, simple or branched, pale brown, septate, subcylindrical, straight or slightly curved, (7.5–)9.5–45(–52.5) × 3–4 µm (av. ± SD = 19.3 ± 10.9 × 3.2 ± 0.3 µm, n = 30). *Conidiogenous cells* terminal or intercalary, flask-shaped to clavate, 5–13.5(–14) × 3–4 µm (av. ± SD = 7.5 ± 2.2 × 3.3 ± 0.3 µm, n = 30), producing conidia sympodially on long open denticles; denticles cylindrical, pale brown, up to 1 µm long. *Conidia* solitary, broadly ellipsoidal with a protuberant hilum, strongly constricted at the septum, 1-septate, brown, finely echinulate to verrucose, sometimes with a wing-like gelatinous brown sheath, released by rhexolytic secession, 7–11(–11.5) × 3.5–5 µm (av. ± SD = 8.4 ± 1.0 × 3.9 ± 0.3 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 16–18 mm diam after 14 d at 26 °C, felty, growing slowly, margin irregular, grey olivaceous. On OA reaching up to 17–18 mm diam, cottony to floccose, immersed, dark brown. On MEA reaching 24–26 mm diam, grey olivaceous, aerial mycelium moderate. On PDA and MEA with ochreous diffusible pigment.

Material examined. China, Guizhou Province, Guiyang City, Huaxi Wetland Park, N26°43'92" E106°67'76", 1140 m a.s.l., isolated from the humus soil in the stream, 16 Nov. 2020, *T.P. Wei* (HGUP 18267), living culture GUCC 18267 = CGMCC 3.20572.

Notes — Multi-locus phylogenetic analyses indicate that our newly obtained isolates GUCC 18267 clustered together with *V. thailandica*, and were sister to *V. terricola*, *V. verruculosa* and *V. cylindricalis*. Morphologically, *V. thailandica* can be readily distinguished from other members of *Verruconis* by its two-celled ellipsoidal conidia with a wing-like gelatinous sheath (Hernández-Restrepo et al. 2020).

Matsushimaea Subramanian, Kavaka 5: 96. 1977 ‘1978’

Type species. *Matsushimaea fasciculata* (Matsush.) Subramanian.

Notes — *Matsushimaea* was introduced by Subramanian (1977) to accommodate species segregated from *Torula* (*T. fasciculata*), which are characterised by the production of sessile, branched and aseptate conidia from polyblastic sympodial conidiogenous cells. This genus was formerly placed in the *Pezizomycotina* as *incertae sedis* (Castañeda-Ruiz et al. 1996, Matsushima 1996). Later, Crous et al. (2018b) using the rDNA (ITS and LSU) sequence data elucidated the phylogenetic position of *Matsushimaea* and placed it in *Sympoventuriaceae*. Presently, *Matsushimaea* includes four species, *M. fasciculata*, *M. fertilis*, *M. magna* and *M. monilioides* (Castañeda-Ruiz et al. 1996, Matsushima 1996, Crous et al. 2018b). Among them, *M. fertilis* and *M. magna* lack authentic cultures and DNA sequence data, thus their phylogenetic position remains unknown.

Matsushimaea fasciculata (Matsush.) Subram., Kavaka 5: 96. 1977 — Fig. 20

Basionym. *Torula fasciculata* Matsush., Icon. Microfung. Matsush. Lect. (Kobe): 153. 1975.

Mycelium superficial or immersed, hyphae branched, septate, pale brown, smooth, occasionally with irregular swellings, 1.5–2 µm wide. *Conidiophores* reduced to conidiogenous cells arising directly from vegetative hyphae. *Conidiogenous cells* integrated, terminal or intercalary, mono- or polyblastic, pale brown, cylindrical to inflated, smooth-walled, 4–5.5 × 4–5 µm (av. ± SD = 4.4 ± 0.4 × 4.1 ± 0.3 µm, n = 30). *Conidia* catenate, usually formed in branched chains, straight to sometimes curved, up to (9.5–)14–50.5(–53) µm (av. ± SD = 27.5 ± 9.5 µm, n = 30) long; cells subglobose or ellipsoidal to somewhat pyriform, sessile or on short protrusions, aseptate, smooth, pale to dark brown, 3.5–5 × 3.5–5 µm (av. ± SD = 3.9 ± 0.4 × 4.1 ± 0.4 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 14–15 mm diam after 14 d at 26 °C, velvety, olivaceous at centre, dark brown at periphery, margin entire. On OA reaching up to 15–19 mm diam, dark brown, dusty, flat, with sparse aerial mycelium. On MEA reaching 15–16 mm diam, olivaceous grey, floccose to loosely cottony.

Material examined. China, Guizhou Province, Guiyang City, Tianhetan Tourist Holiday Resort, N26°43'95" E106°57'64", 1164 m a.s.l., from soil, 16 Apr. 2018, *T.P. Wei* (HGUP 18239), living culture GUCC 18239 = CGMCC 3.20544.

Fig. 20 *Matsushimaea fasciculata* (GUCC 18239). a–c. Colony on PDA, OA and MEA; d–l. conidia in simple or branched chains arising from conidiogenous cells; m–o. olivaceous to plate brown, subglobose or pyriform and smooth-walled conidia. — Scale bars: d, n = 20 µm, all others = 10 µm.

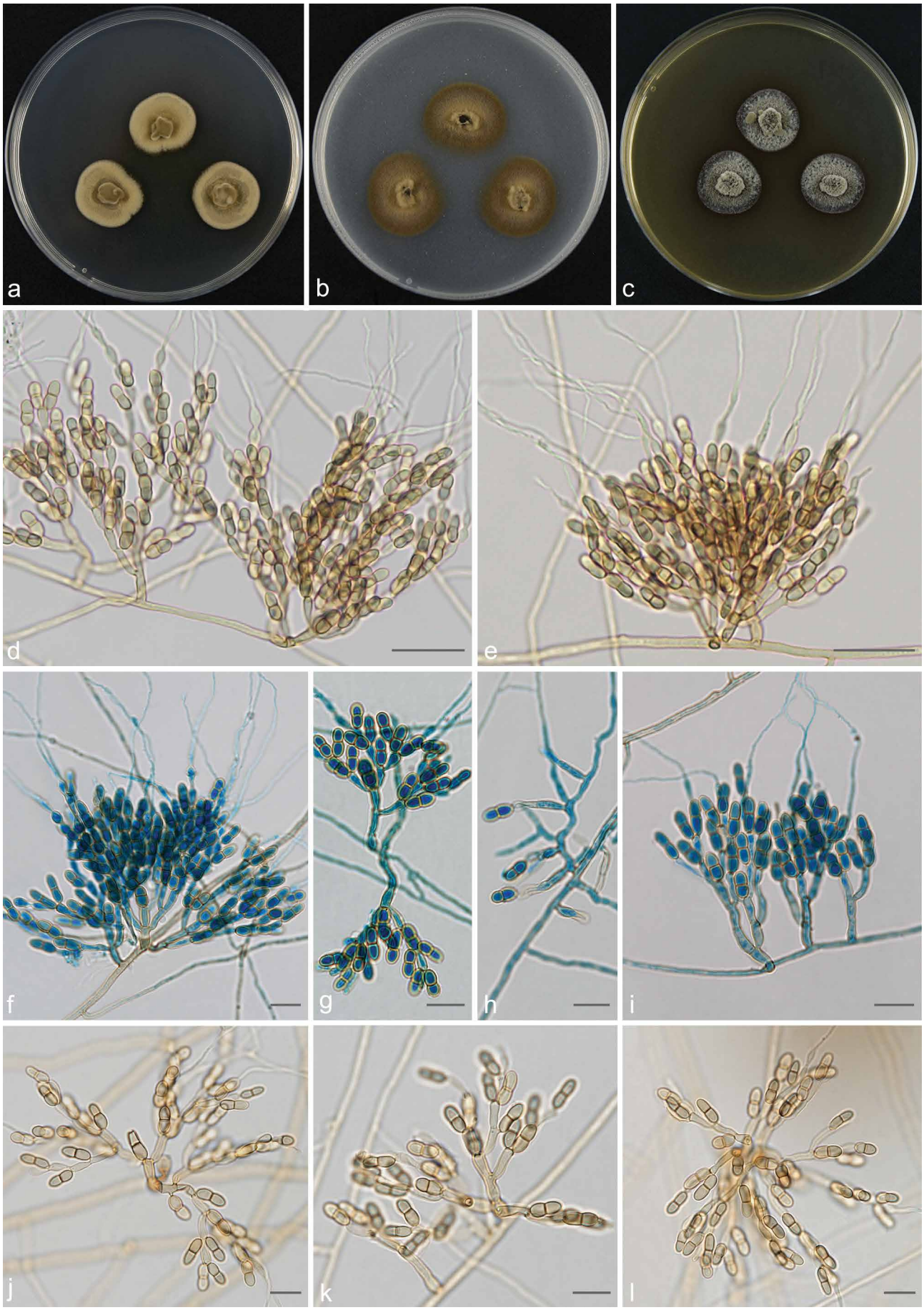

Fig. 21 *Mycosisymbrium cirrhosum* (GUCC 1837). a–c. Colony on PDA, OA and MEA; d–e. filiform appendages terminating from conidiophores; f–i. conidia stained with lactic acid phenol cotton blue; j–l. conidiophore aggregates with conidia. — Scale bars: d–e = 20 µm, all others = 10 µm.

Notes — In this study, the phylogenetic analysis is partly consistent with the morphological comparison, and our isolate GUCC 18239 and *M. fasciculata* have basically the same morphological characteristics (Fig. 1). All members of *Matsushimaea* have been isolated from forest litter and soil, which indicates that the lifestyle of this genus is probably saprophytic (Fig. 3). Moreover, this second report of this poorly known taxon extends its distribution to southwest China from its original location in Japan (Matsushima 1975).

Mycosisymbrium Carris, Mycologia 86: 132. 1994

Type species. *Mycosisymbrium cirrhosum* Carris.

Notes — The monotypic genus *Mycosisymbrium* was first described by Carris (1994), based on *M. cirrhosum* collected from dead leaves of *Vaccinium macrocarpon* in Massachusetts. It is characterised by discrete aggregates of conidiophores terminating in sterile, filiform appendages and brown, 1-septate conidia. Initially, this genus was treated as *incertae sedis* in *Pezizomycotina*. Pratibha & Prabhugaonkar (2016) confirmed the phylogenetic placement of *Mycosisymbrium*, which is a well-supported sister genus to *Ochroconis* and *Verruconis* in *Sympoventuriaceae*. It is noteworthy that since *Mycosisymbrium* was described, only Pratibha & Prabhugaonkar (2016) have reported on this species.

Mycosisymbrium cirrhosum Carris, Mycologia 86: 132. 1994 — Fig. 21

Mycelium consisting of brown, septate, branched, smooth, thick-walled, 1.5–2 µm diam hyphae. *Conidiophores* in determinate clusters, discrete, infundibuliform, pale to dark brown, smooth, branched, each branch terminating in a filiform appendage, (21.5–)24–50(–57.5) × 3–4 µm (av. ± SD = 37.9 ± 9.3 × 3.2 ± 0.3 µm, n = 30); appendages hyaline, flexuous, up to (29–)47–85.5(–90.5) µm (av. ± SD = 63.4 ± 16.9 µm, n = 30) long. *Conidiogenous cells* terminal or intercalary, mono- to polyblastic, cylindrical, pale brown, with one to two denticle-like conidiogenous loci inconspicuous to slightly prominent, (4.5–)5.5–10.5(–11) × (2–)2.5–3.5(–4) µm (av. ± SD = 7.8 ± 1.2 × 2.6 ± 0.3 µm, n = 30). *Conidia* solitary, oblong, 1-septate, smooth-walled, with bluntly rounded ends, constricted at median septum, 9–12 × (3.5–)4–5 µm (av. ± SD = 9.8 ± 0.8 × 4.0 ± 0.3 µm, n = 30).

Culture characteristics — Colonies on PDA attaining 24–27 mm diam after 14 d at 26 °C, margin effuse, brown, with moderate aerial mycelium. On OA reaching up to 16–25 mm diam, mycelium immersed, dark brown, felty or granulose. On MEA reaching 23–24 mm diam, woolly to loosely cottony, olivaceous grey.

Material examined. China, Guizhou Province, Meitan County, N27°41'08" E107°25'41", 910 m a.s.l., isolated from decaying *Camellia sinensis* leaf litter, 10 Aug. 2019, *T.P. Wei* (HGUP 1837), living culture GUCC 1837 = CGMCC 3.20541.

Notes — Multi-locus phylogenetic analyses indicate that our isolate GUCC 1837 clusters with *M. cirrhosum* with high statistical support. Furthermore, the two strains are morphologically similar (Fig. 21). This is the third report of *M. cirrhosum*, which was previously isolated in Massachusetts, USA (Carris 1994) and Goa, India (Pratibha & Prabhugaonkar 2016). In our study we extended its distribution to southwest China and added another new host record.

DISCUSSION

The controversy of Ochroconis, Scolecobasidium and Verruconis

Ochroconis, *Scolecobasidium* and *Verruconis* are morphologically and phylogenetically similar. Historically, there is some disagreement and incongruence about the phylogenetic placement, circumscription and classification of these three genera (De Hoog & Von Arx 1973, Ren et al. 2013, Giraldo et al. 2014, Samerpitak et al. 2014). Although several taxonomic revisions of these genera have been made based on morphology and phylogeny, their species boundaries have not been completely resolved due to historical confusion and limited molecular data (Samerpitak et al. 2016, Qiao et al. 2019, Shen et al. 2020). In this study, our multi-locus phylogenetic analyses indicated that *Scolecobasidium* and *Ochroconis* are synonymous and sister to *Verruconis*, and reside in *Sympoventuriaceae* (Fig. 1, 2). Morphologically, *Verruconis* and *Scolecobasidium* are distinguished mainly based on their conidial shape; in *Verruconis* the conidia are pale to dark brown, verrucose to coarsely ornamented, with protuberant hila, while in *Scolecobasidium* the conidial shape is more variable from ellipsoidal, cylindrical, bilobate, to T- or Y-shaped, and conidia are smooth-walled to verruculose. Additionally, the dark brown diffuse red colony pigmentation on PDA of *Verruconis* also distinguishes this genus from *Scolecobasidium*, which tends to have a pale luteus pigment. The chlamydospores seem to be another taxonomically important feature, in *Scolecobasidium* they are spherical or subcylindrical, smooth-walled, but in *Verruconis* they are cylindrical or clavate, verruculose and larger. Furthermore, *Verruconis* includes thermophilic and mesophilic species, while *Scolecobasidium* only has mesophilic species.

The species boundaries drawn in this study are mainly based on the multi-locus phylogeny as well as morphology. Compared to previous studies, more samples and additional gene markers were used to provide a better understanding of the phylogenetic relationships among species of *Scolecobasidium* and *Verruconis*. By comparing morphological characteristics and related DNA sequence data, seven new species were proposed in *Scolecobasidium* and *Verruconis*, namely *S. camellicola*, *S. coiledmyces*, *S. echinulatum*, *S. obovoideum*, *S. verrucaria*, *S. zunyiense* and *V. cylindricalis*. We also proposed six new combinations in *Scolecobasidium* and *Verruconis* as *S. ferulica*, *S. guangxiensis*, *S. helicteris*, *S. leishanicola*, *S. mirabilis* and *V. tricladiata*. The number of species in *Scolecobasidium* and *Verruconis* has increased significantly over the years (Crous et al. 2019c, Shen et al. 2020). *Scolecobasidium* and *Verruconis* are rather common genera of saprotrophic soil hyphomycetes, some of which are opportunistic neurotropic pathogens of humans, fish or other animals, and some are also known for their thermophilic properties (Samerpitak et al. 2014, 2019). *Scolecobasidium* is the largest genus of *Sympoventuriaceae* with 88 accepted species names recorded in MycoBank (http://www.mycobank.org, April 2022), 39 of which are devoid of DNA sequence data in GenBank. Therefore, to resolve the phylogenetic position of these species in *Scolecobasidium*, they need to be re-collected, sequenced and epitypified.

Genera of Sympoventuriaceae

Sympoventuriaceae was originally established for three groups, namely *Sympoventuria*, *Veronaeopsis* and fusicladium-like species (Zhang et al. 2011). However, as discussed by Zhang et al. (2011), the fusicladium-like morphs are polyphyletic and include species residing in another different family, *Venturiaceae*. Machouart et al. (2014) transferred *Scolecobasidium* (= *Ochroconis*) and *Verruconis* to the *Sympoventuriaceae*, thereby expanding the concept of the family. Subsequent phylogenetic

studies further expanded the concept of *Sympoventuriaceae*, making it the largest family of *Venturiales* (Johnston & Park 2016, Tibpromma et al. 2018, Crous et al. 2019a, Shen et al. 2020). Although these advances have allowed the resolution of several long-standing questions concerning the generic boundaries of *Sympoventuriaceae*, many questions remain unresolved about the phylogenetic relationships of some taxa, especially genera and species for which molecular data are not yet available. To better define the generic boundaries and reveal the evolutionary relationship of *Sympoventuriaceae*, we carried out a more comprehensive analysis of this group based on a hitherto most complete sequence dataset consisting of seven loci (SSU, ITS, LSU, *act1*, *tub2*, *tef1* and *rpb2*). The present results resolved 22 well-supported monophyletic lineages, representing 22 genera (Fig. 1), viz., *Acroconidiellina*, *Bellamyces*, *Clavatispora*, *Echinocatena*, *Fuscohilum*, *Guizhoumyces*, *Helicopsis*, *Matsushimaea*, *Melnikomyces*, *Mycosisymbrium*, *Neocoleroa*, *Neofusicladium*, *Parafusicladium*, *Pinaceicola*, *Pseudosigmoidea*, *Scolecobasidium*, *Sterila*, *Sympoventuria*, *Tropospora*, *Veronaeopsis*, *Verruconis* and *Yunnanomyces*. These included fungi with a broad spectrum of morphology, lifestyles and modes of nutrition, accommodating saprophytes, endophytes, plant pathogens, and animal or human opportunistic pathogens (Samerpitak et al. 2014, 2019, Wang et al. 2018, Crous et al. 2020).

The number of known taxa in *Sympoventuriaceae* is increasing at a steady pace as more geographic areas and habitats are investigated, and its taxonomy has also changed dramatically (Wijayawardene et al. 2014, Tibpromma et al. 2018, Shen et al. 2020). In this study, in addition to the 15 genera previously placed in *Sympoventuriaceae* (Table 4), we also reassessed species of *Acroconidiellina*, *Clavatispora*, *Guizhoumyces*, *Matsushimaea*, *Melnikomyces*, *Mycosisymbrium* and *Yunnanomyces*. The morphological characters and molecular data of these genera provide significant evidence for their taxonomic placement in *Sympoventuriaceae*. In the multi-locus phylogenetic tree of the current study, *A. arecae* is allied with *Scolecobasidium* at the top of the clade (Fig. 1). Nevertheless, *A. arecae* can be distinguished morphologically from the species in *Scolecobasidium* by its multi-septate, obclavate, large conidia with a truncate base and macronematous conidiophores (Li et al. 2016). The placement of *Acroconidiellina* in *Sympoventuriaceae* contradicts earlier placements in the order *Pleosporales* due to similarities in the type of conidiophores and conidium morphology (Ellis 1971, Zhang et al. 2009, Bhat 2010). Therefore, our results are more in line with the proposal of Hernández-Restrepo et al. (2016) about a closer affinity with members of the *Sympoventuriaceae*. Furthermore, our findings support the placement of *Mycosisymbrium* in *Sympoventuriaceae*, as suggested by previous molecular studies (Pratibha & Prabhugaonkar 2016). The extended taxon sampling and the use of five markers allow us to strongly corroborate these findings. Species of two genera were included in the analyses, *Mycosisymbrium* and *Clavatispora*, which formed two different sister subclades (Fig. 1). *Mycosisymbrium* can be distinguished by having discrete aggregates of conidiophores terminating in sterile, filiform appendages and 1-septate conidia (Fig. 21), while *Clavatispora* has 1(–3)-septate, guttulate conidia that are deeply constricted at their septa (Boonmee et al. 2014). *Clavatispora* also produced a sexual morph in culture characterised by ostiolate ascomata, bitunicate asci and muriformly septate ascospores.

According to the multigene phylogeny and morphology in the present study, a new genus, *Guizhoumyces*, is now recognised within *Sympoventuriaceae* (Fig. 1). Morphologically, members of *Guizhoumyces* are quite distinct from those of *Sympoventuriaceae*, having straight or curved, smooth and acicular to obclavate conidia, which contrasts with the mostly verrucose to denticulate and subcylindrical to fusoid-ellipsoidal conidia typical for species of other genera; as well as by the presence of anastomosis between mature conidia in *Guizhoumyces*. Moreover, *Matsushimaea* forms a robust clade with another two genera, *Fuscohilum* and *Neocoleroa* (Fig. 1). As we mentioned before, our results confirm its placement within *Sympoventuriaceae*, although the DNA sequences of *M. fertilis* and *M. magna* were not available. The polyblastic and sympodial conidiogenous cells of several other genera in *Sympoventuriaceae* share similar morphologies with those of *Matsushimaea*. However, *Matsushimaea* differs in having sessile, branched and aseptate conidia arising directly from vegetative hyphae (Crous et al. 2018b; Fig. 20), which strongly supports the genus as monophyletic. Based on the general characteristics of *Melnikomyces*, previous studies hypothesized its close relationship with *Scolecobasidiella* and *Scolecobasidium* (Crous et al. 2014, Hernández-Restrepo et al. 2020). In our phylogenetic tree, *Melnikomyces* formed a separate clade in *Sympoventuriaceae* distinct from other genera (Fig. 1). Morphologically, this genus has certain similarities with *Scolecobasidiella* and *Scolecobasidium*, but can be distinguished from them by its fusoid-ellipsoidal conidia and the chlamydospores that are subglobose, occurring in branched chains (Wei et al. 2020). Thus, our analysis shows that the phylogenetic isolation of *Melnikomyces*, *Scolecobasidiella* and *Scolecobasidium* may be supported by the unique morphological features and genetic differences. *Yunnanomyces* is characterised by its globose to broadly oval, yellow to brown and muriformly septate conidia (Tibpromma et al. 2018). This genus is phylogenetically related to the monotypic genus *Sterila*, and formed a well-supported clade within *Sympoventuriaceae* (Fig. 1). Morphologically it is not possible to compare these two genera, as the latter is sterile in culture. Nonetheless, *Yunnanomyces* differs from its closest phylogenetic neighbour *Sterila* by unique fixed alleles in four loci of their type species, by 6 bp in ITS (3 %), 52 bp in LSU (7 %), 278 bp in *tub2* (57 %) and 191 bp in *rpb2* (24 %). More specifically, these two genera represent significantly different lineages in *Sympoventuriaceae*.

Sympoventuria currently includes three species, namely *S. africana*, *S. capensis* and *S. melaleucae*, with the sexual species *S. capensis* designated as the generic type (Crous et al. 2007a, 2017). *Sympoventuria* is phylogenetically closely related to the asexual genus *Helicopsis* with high support from three independent algorithms (Fig. 1). *Sympoventuria* is, however, clearly distinguished from other asexual morphs by its fusoid-ellipsoid or cylindrical, simple or branched conidial chains (helically coiled conidia with thick conidial filaments in *Helicopsis*) (Karsten 1888, Crous et al. 2007b, Tsui & Berbee 2010). Furthermore, *Neocoleroa metrosideri*, a little-known sexual morph is here shown to be closely related to the sterile *N. cameroonensis*. However, *N. metrosideri* differs from its closest phylogenetic neighbour *N. cameroonensis* by unique fixed alleles in two loci, by 56 bp in ITS (14 %) and 26 bp in LSU (3 %). Notably, species with sexual morphs were scattered throughout the phylogenetic tree, which indicates that sexual reproduction may have evolved more than once within the family (Fig. 1). Overall, the results of this study have provided a robust overview of the species boundaries in *Sympoventuriaceae*. This is based largely on seven gene regions inferring an updated phylogram of all concerned genera in the family. On the other hand, multi-gene phylogenetic analyses combined with morphological features provide a robust means to delimit fungal species boundaries (Woudenberg et al. 2017, Lücking et al. 2020, Crous et al. 2021). Results of this study revealed that SSU, ITS, LSU, *act1*, *tub2*, *tef1* and *rpb2* gene regions can provide stable and reliable resolution for species delimitation

in *Sympoventuriaceae*. Although each of these loci proved to be suitable barcoding markers for species identification, a combined analysis is highly recommended.

Evolution of lifestyles in Sympoventuriaceae

The transition from saprophytes to endophytes, plant pathogens and animal or human opportunistic pathogens is a notable feature within *Sympoventuriaceae* (Fig. 3). Studies have shown that the saprotrophic fungal ancestors experienced a large-scale loss of plant cell wall degrading enzymes, and obtained effector-like secreted proteins to fit a plant-fungal associated lifestyle (Bödeker et al. 2014, Kohler et al. 2015, Martin et al. 2016, Haridas et al. 2020, Shen et al. 2020, Benavent 2021). In our reconstruction analyses, although the *Sympoventuriaceae* clade most conspicuously includes saprophytes, members of the *Neocoleroa* and *Sterila* clades convergently evolved towards plant pathogens and animal/human opportunistic pathogens, with a shift towards endophytes in *Verruconis* (Fig. 3). In addition, we found the *Scolecobasidium* clade to have a high species richness, including saprophytes, endophytes, animal/human opportunistic and plant pathogens, and to be associated with significant increasing shifts in diversification rate (Fig. 3). It is worth noting that transition from saprophytes to plant pathogens and animal or human opportunistic pathogens has independently occurred multiple times during the evolution of *Sympoventuriaceae*, which is possibly driven by habitat selection (Fig. 3). The present study has provided a wealth of data about the lifestyle and phylogeny of *Sympoventuriaceae*, showing some trends in the evolution of species in the family. For example, saprophytes were mainly at the early diverged clades in phylogenetic trees, e.g., *Neofusicladium*, *Parafusicladium*, *Pseudosigmoidea* and *Veronaeopsis*. In contrast, the endophytes, plant pathogens and animal/human opportunistic pathogens were only found in the *Acroconidiellina*, *Neocoleroa*, *Scolecobasidium*, *Sterila* and *Verruconis* species in more recently diverged clades, supporting a strong correlation between the evolution of *Sympoventuriaceae* life strategies and its phylogeny.

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