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Novel collophorina-like genera and species from *Prunus* trees and vineyards in Germany

S. Bien[1], C. Kraus[2], U. Damm[1]

Key words

Collophora
morphology
multi-locus phylogeny
new taxa
species diversity
systematics

Abstract Strains with a yeast-like appearance were frequently collected in two surveys on the biodiversity of fungi in Germany, either associated with necroses in wood of *Prunus* trees in orchards in Saxony, Lower Saxony and Baden-Württemberg or captured in spore traps mounted on grapevine shoots in a vineyard in Rhineland-Palatinate. The morphology of the strains was reminiscent of the genus *Collophorina*: all strains produced aseptate conidia on integrated conidiogenous cells directly on hyphae, on discrete phialides, adelophialides and by microcyclic conidiation, while in some strains additionally endoconidia or conidia in conidiomata were observed. Blastn searches with the ITS region placed the strains in the *Leotiomycetes* close to *Collophorina* spp. Analyses based on morphological and multi-locus sequence data (LSU, ITS, *EF-1α*, *GAPDH*) revealed that the 152 isolates from wood of *Prunus* spp. belong to five species including *C. paarla*, *C. africana* and three new species. A further ten isolates from spore traps belonged to seven new species, of which one was isolated from *Prunus* wood as well. However, a comparison with both LSU and ITS sequence data of these collophorina-like species with reference sequences from further *Leotiomycetes* revealed the genus *Collophorina* to be polyphyletic and the strains to pertain to several genera within the *Phacidiales*. *Collophorina paarla* and *C. euphorbiae* are transferred to the newly erected genera *Pallidophorina* and *Ramoconidiophora*, respectively. The new genera *Capturomyces*, *Variabilispora* and *Vexillomyces* are erected to accommodate five new species isolated from spore traps. In total nine species were recognised as new to science and described as *Collophorina badensis*, *C. germanica*, *C. neorubra*, *Capturomyces funiculosus*, *Ca. luteus*, *Tympanis inflata*, *Variabilispora flava*, *Vexillomyces palatinus* and *V. verruculosus*.

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INTRODUCTION

The coelomycetous genus *Collophora* (*Tympanidaceae*, *Phacidiales*, *Leotiomycetes*) was described from necrotic wood of several *Prunus* species (*P. dulcis*, *P. persica*, *P. persica* var. *nucipersica*, *P. salicina*) in South Africa (Damm et al. 2010). After the previously described plant genus *Collophora* Mart. 1830 (*Apocynaceae*) was incorporated in the plant list, the fungal name was recognised as illegitimate being a later homonym (Art. 53.1, McNeill et al. 2015) and renamed as *Collophorina* (Wijayawardene et al. 2017). Five species were originally described by Damm et al. (2010) based on a combination of morphological and DNA sequence data, namely *C. africana*, *C. capensis*, *C. paarla*, *C. pallida* and *C. rubra*. However, based on multi-locus sequence data, *C. pallida* and *C. capensis* were later synonymised with *C. paarla* and *C. africana*, respectively (Gramaje et al. 2012). A further three species have subsequently been described, namely *C. hispanica* from *P. dulcis* in Spain (island of Mallorca), *C. aceris* from *Acer glabrum* var. *douglasii* in the North West of the USA and *C. euphorbiae* from *Euphorbia polycaulis* in Iran (Gramaje et al. 2012, Xie et al. 2013, Nasr et al. 2018).

Collophorina spp. (mostly as *Collophora*) have also been reported from necrotic and symptomless wood and leaves of *Prunus* spp. in Germany, Iran, Slovakia and Spain (Benavides et al. 2013, Ivanová & Bernadovičová 2013, Aghdam & Fotouhifar 2016, Arzanlou et al. 2016, Gierl & Fischer 2017), from necrotic wood of *Castanea sativa* (Yurkewich et al. 2017), from leaves of forest trees and grapevine in France (Fort et al. 2016) and from roots of *Caluna vulgaris* and *Holcus lanatus* in Germany (Kreyling et al. 2012). In addition to plant hosts, there is also one report of *Collophorina* from an animal, namely from the beak of a hummingbird (Belisle et al. 2012). *Collophorina* species were also repeatedly isolated from spore traps (Fischer et al. 2016, Fort et al. 2016, Gierl & Fischer 2017).

Species of *Collophorina* produce whitish, cream or red pigmented colonies and aseptate conidia originating from reduced conidiogenous cells resembling those of the genus *Coniochaeta* (syn. *Lecythophora*), from conidiomata or by microcyclic conidiation. A sexual morph has not been observed. Sanoamuang et al. (2013) discussed *Gelatinomyces* as possible sexual morph of *Collophorina*, but dismissed this assumption after a thorough molecular and morphological comparison.

In two surveys aiming to reveal the diversity of fungi either associated with wood necroses of *Prunus* trees in Germany or captured in spore traps in vineyards in Germany, fungi with a yeast-like appearance and reduced conidiogenous cells were frequently isolated that were tentatively placed in the genus *Collophorina* by ITS sequence comparison. The objective of this study was to investigate the phylogenetic relationships of these strains using molecular phylogenetic analyses of LSU, ITS, *EF-1α* and *GAPDH* sequences and to characterise the species based on molecular, morphological and physiological data.

MATERIALS AND METHODS

Sampling and fungal isolation

Branches with symptomatic wood (e.g., canker, necroses, wood streaking, damaged bark, gummosis) were sampled from plum

[1] Senckenberg Museum of Natural History Görlitz, Department Botany, Section Mycology, PF 300 154, 02806 Görlitz, Germany; corresponding author e-mail: steffen.bien@senckenberg.de.
[2] Julius Kühn-Institute (JKI), Federal Research Centre of Cultivated Plants, Geilweilerhof, 76833 Siebeldingen, Germany.

Table 1 List of strains included in this study, with collection details and GenBank accession numbers.

Species	Accession no.[1]	Host / substrate	Country	GenBank no.[2]				References
				LSU	ITS	*EF-1α*	*GAPDH*	
Alatospora acuminata	CCM F-02383	stream foam	Great Britain	KC834018	AY204587	–	–	Baschien et al. (2013)
Alatospora pulchella	CCM F-502*	stream, *Athyrium filix-femina* frond	Czech Republic	KC834019	KC834039	–	–	Baschien et al. (2013)
Aotearoamyces nothofagi	ICMP 21868	unidentified wood	New Zealand	MG807386	KM677202	–	–	Quijada et al. (2018)
	PDD 106298	*Nothofagus fusca*, bark of dead wood	New Zealand	MG807388	MG807392	–	–	Quijada et al. (2018)
Cadophora luteo-olivacea	CBS 141.41*	waste water	Sweden	MH867586	AY249066	KM497089	JN808849	Harrington & McNew (2003)
Capturomyces funiculosus	GLMC 1846*	spore trap on *Vitis vinifera*	Germany	**MK314599**	**MK314552**	**MK314517**	**MK314493**	This study
	GLMC 1848	spore trap on *Vitis vinifera*	Germany	**MK314600**	**MK314553**	**MK314518**	**MK314494**	This study
Capturomyces luteus	GLMC 1842*	spore trap on *Vitis vinifera*	Germany	**MK314603**	**MK314554**	**MK314519**	**MK314495**	This study
Claussenomyces olivaceus	NB-479	*Picea rubens*, resin on branch stub	Canada	KY633629	KY633590	–	–	Tanney & Seifert (2018)
Claussenomyces prasinulus	KL218	rotten wood	Estonia	KX090815	–	–	–	Pärtel et al. (2017)
'*Collophorina*' *aceris*	PC 23	*Acer glabrum* var. *douglasii*	USA	–	KF057075	–	–	Xie et al. (2013)
Collophorina africana	CBS 120872*	*Prunus salicina*, necrotic wood	South Africa	**MK314588**	GQ154570	GQ154643	GQ154648	Damm et al. (2010), this study
	CBS 120879	*Prunus salicina*, necrotic wood	South Africa	GQ154610	GQ154571	GQ154644	GQ154649	Damm et al. (2010)
	GLMC 1736	*Prunus domestica*, necrotic wood	Germany	**MK314581**	**MK314542**	**MK314507**	**MK314474**	This study
	GLMC 1777	*Prunus domestica*, necrotic wood	Germany	**MK314582**	**MK314543**	**MK314508**	**MK314475**	This study
	GLMC 462	*Prunus domestica*, necrotic wood	Germany	**MK314583**	**MK314537**	**MK314504**	**MK314470**	This study
	GLMC 464	*Prunus domestica*, necrotic wood	Germany	**MK314584**	**MK314538**	**MK314509**	**MK314471**	This study
	GLMC 466	*Prunus domestica*, necrotic wood	Germany	**MK314586**	**MK314540**	**MK314505**	**MK314476**	This study
	GLMC 551	*Prunus domestica*, necrotic wood	Germany	**MK314585**	**MK314539**	**MK314510**	**MK314472**	This study
	GLMC 600	*Prunus domestica*, necrotic wood	Germany	**MK314587**	**MK314541**	**MK314506**	**MK314473**	This study
Collophorina badensis	GLMC 1684*	*Prunus domestica*, healthy wood	Germany	**MK314594**	**MK314546**	**MK314503**	**MK314482**	This study
	GLMC 1686	*Prunus domestica*, necrotic wood	Germany	**MK314591**	**MK314547**	**MK314502**	**MK314483**	This study
	GLMC 1546	*Prunus domestica*, necrotic wood	Germany	**MK314589**	**MK314544**	**MK314499**	**MK314479**	This study
	GLMC 1637	*Prunus domestica*, necrotic wood	Germany	**MK314590**	**MK314545**	**MK314500**	**MK314480**	This study
	GLMC 1639	*Prunus domestica*, necrotic wood	Germany	**MK314592**	**MK314549**	**MK314501**	**MK314481**	This study
	GLMC 1844	spore trap on *Vitis vinifera*	Germany	**MK314593**	**MK314548**	**MK314498**	**MK314484**	This study
Collophorina germanica	GLMC 1445*	*Prunus avium*, necrotic wood	Germany	**MK314595**	**MK314550**	**MK314515**	**MK314477**	This study
	GLMC 1769	*Prunus avium*, necrotic wood	Germany	**MK314596**	**MK314551**	**MK314516**	**MK314478**	This study
Collophorina hispanica	CBS 128568*	*Prunus dulcis*, branch	Spain	**MK314597**	MH864962	JN808852	JN808845	Gramaje et al. (2012), this study
	CBS 128566	*Prunus dulcis*, branch	Spain	–	JN808839	JN808850	JN808843	Gramaje et al. (2012)
	CBS 128569	*Prunus dulcis*, branch	Spain	MH876412	JN808842	JN808853	JN808846	Gramaje et al. (2012)
Collophorina neorubra	GLMC 929*	*Prunus avium*, necrotic wood	Germany	**MK314604**	**MK314533**	**MK314511**	**MK314485**	This study
	GLMC 1669	*Prunus avium*, necrotic wood	Germany	**MK314606**	**MK314536**	**MK314514**	**MK314488**	This study
	GLMC 1587	*Prunus avium*, necrotic wood	Germany	**MK314605**	**MK314534**	**MK314512**	**MK314486**	This study
	GLMC 1588	*Prunus avium*, necrotic wood	Germany	**MK314607**	**MK314535**	**MK314513**	**MK314487**	This study
Collophorina rubra	CBS 120873*	*Prunus persica*, necrotic wood	South Africa	**MK314598**	GQ154547	JN808855	JN808848	Damm et al. (2010), Gramaje et al. (2012), this study
	CBS 121441	*Prunus persica* var. *nucipersica*, necrotic wood	South Africa	GQ154607	GQ154551	GQ154642	GQ154647	Damm et al. (2010)
Crinula caliciiformis	AFTOL-ID 272	N/A	N/A	AY544680	KT225524	–	–	Lutzoni et al. (2004)
Epiglia gloeocapsae	M193	moss	Finland	EU940128	EU940204	–	–	Stenroos et al. (2010)
Epithamnolia xanthoriae	HA92	N/A	Iceland	KY814508	KY814526	–	–	Suija et al. (2017)
	HA90	N/A	Netherlands	KY814513	KY814532	–	–	Suija et al. (2017)
Flagellospora curvula	CB-M13	*Cladrastis kentukea*, submerged leaf	USA	KC834024	KC834045	–	–	Baschien et al. (2013)
Flagellospora leucohynchus	CCM F-14183	stream foam	Slovakia	KC834025	KC834049	–	–	Baschien et al. (2013)
Gelatinomyces siamensis	KKUK1*	*Bambusa nutans*	Thailand	JX219381	JX219379	–	–	Sanoamuang et al. (2013)
	KKUK2	*Bambusa nutans*	Thailand	JX219382	JX219380	–	–	Sanoamuang et al. (2013)
Gorgomyces honrubiae	CCM F-12003*	stream foam	Spain	KC834028	KC834057	–	–	Baschien et al. (2013)
Holwaya mucida	AFTOL-ID 272	N/A	N/A	AY544680	KT225524	–	–	Lutzoni et al. (2004)
	B 70 0009352	N/A	N/A	DQ257356	DQ257357	–	–	Wang et al. (2006)

Table 1 (cont.)

Species	Accession no.[1]	Host / substrate	Country	GenBank no.[2] LSU	ITS	*EF-1α*	*GAPDH*	References
Mniaecia jungermanniae	M145	moss	Finland	EU940109	EU940185	–	–	Stenroos et al. (2010)
Mniaecia nivea	M167	moss	Finland	EU940115	EU940188	–	–	Stenroos et al. (2010)
Pallidophorina paarla	CBS 120877*	*Prunus salicina*, necrotic wood	South Africa	**MK314610**	GQ154586	GQ154646	GQ154651	Damm et al. (2010), this study
	CBS 120878	*Prunus salicina*, necrotic wood	South Africa	GQ154611	GQ154575	JN808854	JN808847	Damm et al. (2010), Gramaje et al. (2012)
	GLMC 452	*Prunus cerasus*, healthy wood	Germany	**MK314608**	**MK314555**	**MK314524**	**–**	This study
	GLMC 1282	*Prunus domestica*, necrotic wood	Germany	**MK314609**	**MK314561**	**MK314529**	**–**	This study
	GLMC 780	*Prunus domestica*, necrotic wood	Germany	**MK314611**	**MK314559**	**MK314525**	**–**	This study
	GLMC 791	*Prunus cerasus*, necrotic wood	Germany	**MK314612**	**MK314560**	**MK314527**	**–**	This study
	GLMC 892	*Prunus avium*, necrotic wood	Germany	**MK314614**	**MK314556**	**MK314528**	**–**	This study
	GLMC 1230	*Prunus avium*, necrotic wood	Germany	**MK314615**	**MK314557**	**MK314526**	**–**	This study
	GLMC 1497	*Prunus avium*, necrotic wood	Germany	**MK314613**	**MK314558**	**MK314530**	**–**	This study
Ramoconidiophora euphorbiae	CBS 141018*	*Euphorbia polycaulis*	Iran	**MK314602**	MG592739	MG592735	MG592733	Nasr et al. (2018), this study
	IBRC-M 30208	*Euphorbia polycaulis*	Iran	**MK314601**	MG592740	MG592736	MG592734	Nasr et al. (2018), this study
Tympanis abietina	CBS 350.55	*Abies balsamea*	Canada	**MK314617**	**MK314563**	**–**	–	This study
Tympanis acericola	CBS 351.55[aut]	*Acer spicatum*	Canada	**MK314631**	**MK314564**	**–**	–	This study
'*Tympanis*' *alnea*	CBS 352.55	*Alnus*	Canada	**MK314635**	**MK314580**	**–**	–	This study
Tympanis amelanchieris	CBS 353.55*	*Amelanchier*	Canada	MH869048	MH857508	–	–	Vu et al. (2019)
Tympanis confusa	CBS 354.55	*Pinus resinosa*	USA	**MK314619**	**MK314568**	**–**	–	This study
Tympanis conspersa	CBS 355.55	*Malus sylvestris*	USA	**MK314618**	**MK314573**	**–**	–	This study
Tympanis diospyri	CBS 356.55*	*Diospyros virginana*	USA	MH869049	MH857509	–	–	Vu et al. (2019)
Tympanis fasciculata	CBS 357.55	*Viburnum cassioides*	Canada	**MK314620**	**MK314565**	**–**	–	This study
Tympanis hansbroughiana	CBS 358.55*	*Pseudotsuga menziesii*	USA	MH869050	MH857510	–	–	Vu et al. (2019)
Tympanis inflata	GLMC 1856*	spore trap on *Vitis vinifera*	Germany	**MK314625**	**MK314566**	**MK314532**	**MK314496**	This study
Tympanis laricina	CBS 360.55	*Larix laricina*	Canada	**MK314621**	**MK314570**	**–**	–	This study
'*Tympanis*' *malicola*	CBS 221.69	*Malus sylvestris*	Netherlands	**MK314632**	**MK314579**	**–**	–	This study
Tympanis piceae	CBS 361.55*	*Picea glauca*	Canada	MH869051	MH857511	–	–	Vu et al. (2019)
Tympanis piceina	CBS 362.55[aut]	*Picea abies*	Sweden	MH869052	MH857512	–	–	Vu et al. (2019)
Tympanis pitya	CBS 363.55	*Pinus resinosa*	USA	**MK314623**	**MK314569**	**–**	–	This study
Tympanis prunicola	CBS 364.55[aut]	*Prunus*	Canada	MH869053	MH857513	–	–	Vu et al. (2019)
'*Tympanis*' *pseudotsugae*	CBS 365.55*	*Pseudotsuga menziesii*	USA	**MK314633**	MH857514	–	–	Vu et al. (2019), this study
	CBS 463.59	*Pseudotsuga menziesii*	Canada	**MK314634**	**MK314578**	**–**	–	This study
Tympanis saligna	CBS 366.55	*Salix discolor*	Canada	**MK314626**	**MK314567**	**–**	–	This study
Tympanis spermatiospora	CBS 367.55	*Populus*	Canada	**MK314624**	**MK314571**	**–**	–	This study
Tympanis truncatula	CBS 368.55	*Abies balsamea*	Canada	**MK314622**	**MK314572**	**–**	–	This study
Tympanis tsugae	CBS 369.55*	*Tsuga canadensis*	Canada	MH869054	MH857515	–	–	Vu et al. (2019)
'*Tympanis*' *xylophila*	CBS 133220	*Fraxinus excelsior*, decayed branch	Luxembourg	MH877529	MH866059	–	–	Vu et al. (2019)
Variabilispora flava	GLMC 1858*	spore trap on *Vitis vinifera*	Germany	**MK314616**	**MK314562**	**MK314531**	**MK314497**	This study
Vexillomyces palatinus	GLMC 1852*	spore trap on *Vitis vinifera*	Germany	**MK314627**	**MK314574**	**MK314520**	**MK314489**	This study
Vexillomyces verruculosus	GLMC 1854*	spore trap on *Vitis vinifera*	Germany	**MK314629**	**MK314576**	**MK314522**	**MK314492**	This study
	GLMC 1840	spore trap on *Vitis vinifera*	Germany	**MK314630**	**MK314577**	**MK314523**	**MK314491**	This study
	GLMC 1838	spore trap on *Vitis vinifera*	Germany	**MK314628**	**MK314575**	**MK314521**	**MK314490**	This study

[1] AFTOL: Assembling the Fungal Tree of Life project, USA; CBS: Culture collection of the Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; GLMC: Culture collection of Senckenberg Museum of Natural History Görlitz, Görlitz, Germany; IBRC: Iranian Biological Center, Tehran, Iran; ICMP: International Collection of Microorganisms from Plants, Auckland, New Zealand; KKUK: Culture collection of Khon Kaen University, Khon Kaen, Thailand; PDD: New Zealand Fungal Herbarium, Auckland, New Zealand

[2] LSU: nuclear large subunit ribosomal DNA; ITS: internal transcribed spacers and intervening 5.8S nrDNA; *EF-1α*: translation elongation factor 1-α gene; *GAPDH*: partial glyceraldehyde-3-phosphate dehydrogenase gene. Sequences generated in this study are emphasised in **bold**. *ex-type cultures; [aut]authentic strains; N/A not available.

(*P. domestica*), sour cherry (*P. cerasus*) and sweet cherry (*P. avium*) orchards in Saxony, Lower Saxony and Baden-Württemberg, Germany, in 2015 and 2016. Wood pieces (5 × 5 × 5 mm) from the transition zone of symptomatic to non-symptomatic wood tissue as well as pieces of the same size from non-symptomatic wood of the same branch were surface sterilised (30 s in 70 % ethanol, 1 min in 3.5 % NaOCl, 30 s in 70 % ethanol) washed for 1 min in sterilised water and plated on synthetic nutrient-poor agar medium (SNA, Nirenberg 1976) as well as oatmeal agar medium (OA; Crous et al. 2009), both supplemented with 100 mg/L penicillin, 50 mg/L streptomycin sulphate and 1 mg/L chloramphenicol.

Additionally, glass slides covered with petroleum jelly (Balea Vaseline, DM, Karlsruhe, Germany) were attached to vines of *Vitis vinifera* in a research vineyard of Julius-Kühn-Institute Siebeldingen, Rhineland-Palatinate, Germany, in 2016 and 2017. The slides were exchanged on a weekly basis and washed for 10 s with 30 mL washing solution (8 g/L NaCl, 0.2 g/L KCl, 1.44 g/L Na_2HPO_4, 0.24 g/L KH_2PO_4, 0.01 % Tween® 80) followed by filtration first with a 5 µm filter, followed by a 0.45 µm filter. Further 500 µL washing solution were used for washing off the spores and particles from the 0.45 µm filter that were subsequently plated out on each two malt-yeast agar plates (MYA, 250 µL per plate; Crous et al. 2009).

After incubation for several days at 25 °C, hyphal tips of developing fungi were transferred to SNA medium with a sterilised needle. Single-conidial isolates were obtained from the strains for further study. Reference strains are maintained in the culture collections of the Senckenberg Museum of Natural History Görlitz, Germany (GLMC), the Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands (CBS) and the German Collection of Microorganisms and Cell Cultures, Braunschweig, Germany (DSMZ). Specimens (dried cultures), including type specimens were deposited in the fungarium of Senckenberg Museum of Natural History Görlitz (GLM).

Morphological analysis

To enhance sporulation autoclaved filter paper and double-autoclaved pine needles were placed on the surface of the SNA medium. The cultures were incubated at 25 °C. Colony growth on SNA and OA were noted after 2 and 4 wk, colony characters on SNA and OA were noted after 4 wk. Colony colours were rated according to Rayner (1970). Microscopic preparations were made after 4 wk in clear lactic acid and observations and measurements (30 measurements per structure) were made with a Nikon SMZ18 stereomicroscope (SM) or with a Nikon Eclipse N*i*-U light microscope with differential interference contrast (LM). Photographic images were captured with Nikon Digital Sight DS-Fi2 cameras installed on the above-mentioned microscopes making use of the Nikon NIS-Elements software (v. 4.30).

Phylogenetic analysis

Genomic DNA of the isolates was extracted using the method of Damm et al. (2008). A partial sequence of the 28S nrDNA (LSU) and the 5.8S nuclear ribosomal gene with the two flanking internal transcribed spacers ITS-1 and ITS-2 were amplified and sequenced using the primer pairs LROR (Rehner & Samuels 1994) + LR5 (Vilgalys & Hester 1990) and ITS-1F (Gardes & Bruns 1993) + ITS-4 (White et al. 1990), respectively. Additionally, a partial sequence of the translation elongation factor 1α (*EF-1α*) and a 200-bp intron of the glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*) were amplified using the primer pairs EF1-728F + EF1-986R (Carbone & Kohn 1999) and GDF1 + GDR1 (Guerber et al. 2003), respectively.

The reaction mixture for PCR contained 1 µL of 1 : 10 DNA template, 2.5 µL 10× buffer (Peqlab, Erlangen, Germany), 1 µL of each primer (10 mM), 2.5 µL $MgCl_2$ (25 mM), 0.1 µL *Taq* polymerase (0.5U, Peqlab, Erlangen, Germany) and 2.5 µL of 2 mM dNTPs. Each reaction was made up to a final volume of 20 µL with sterile water. DNA amplifications of ITS were carried out in a Mastercycler® pro S (Eppendorf, Hamburg, Germany) programmed for an initial denaturation at 95 °C for 5 min, followed by 30 cycles of 94, 51 and 72 °C for 30, 30 and 60 s, respectively, with a 3 min extension at 72 °C on the final cycle. For DNA amplifications of LSU the PCR conditions were set according to Paulin & Harrington (2000). The PCR conditions for the amplification of the *EF-1α* and *GAPDH* were those as described in the respective references listed above. The PCR products were visualised on a 1 % agarose gel and sequenced by the Senckenberg Biodiversity and Climate Research Centre (BiK-F) laboratory (Frankfurt, Germany). The forward and reverse sequences were assembled by using BioEdit Sequence Alignment Editor (v. 7.2.5; Hall 1999).

Sequences of all *Collophorina* species as well as other reference sequences of *Leotiomycetes*, especially those of the ex-type strains, were downloaded from GenBank and added to the sequences generated in this study and those of the outgroup *Cadophora luteo-olivacea* CBS 141.41. Two sequence datasets were compiled. In dataset 1 the sequences from this study as well as sequences of *Collophorina* species were combined with other sequences from *Leotiomycetes* for a two gene phylogeny (LSU, ITS) to resolve the generic placement of the strains. In dataset 2 the sequences generated in this study were combined with sequences from all formerly described species of *Collophorina* for a four gene phylogeny (LSU, ITS, *EF-1α*, *GAPDH*) to determine species identification. The datasets were aligned automatically using MAFFT v. 7.308 (Katoh et al. 2002, Katoh & Standley 2013) and manually adjusted where necessary.

The phylogenetical analyses were conducted using Bayesian Inference (BI), Maximum Likelihood (ML) and maximum parsimony (MP). For BI analyses, the best fit model of evolution was estimated by MEGA7 (Kumar et al. 2016) for each partition. Posterior probabilities were determined by Markov Chain Monte Carlo sampling (MCMC) in MrBayes v. 3.2.6 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) as implemented in Geneious v. 10.2.2 (Kearse et al. 2012), using the estimated models of evolution. Four simultaneous Markov chains were run for 1 Mio generations and trees were sampled every 100th generation. The first 2 000 trees, which represent the burn-in phase of the analyses, were discarded and the remaining 8 000 trees were used to calculate posterior probabilities in the majority rule consensus tree. The ML analyses were performed by RAxML v. 8.2.11 (Stamatakis 2006, 2014) as implemented in Geneious v. 10.2.2 (Kearse et al. 2012) using the GTRGAMMA model with the rapid bootstrapping and search for best scoring ML tree algorithm including 1 000 bootstrap replicates. The MP analyses were performed with MEGA7 (Kumar et al. 2016) using tree-bisection-reconnection (TBR) as branch-swapping algorithm. The robustness of the trees was evaluated by 1 000 bootstrap replicates and 10 random sequence additions. Tree length, consistency index, retention index and composite index were calculated for the resulting trees. The DNA sequences generated in this study were deposited in GenBank (Table 1), the alignments in TreeBASE (https://treebase.org/treebase-web/home.html) (23717) and taxonomic novelties in MycoBank (www.mycobank.org; Crous et al. 2004).

RESULTS

Phylogenetic analyses

In total 152 out of 1 018 isolates from necrotic wood of *Prunus* spp. and 10 out of 810 isolates from spore traps mounted on grapevine vines were tentatively identified as *Collophorina* spe-

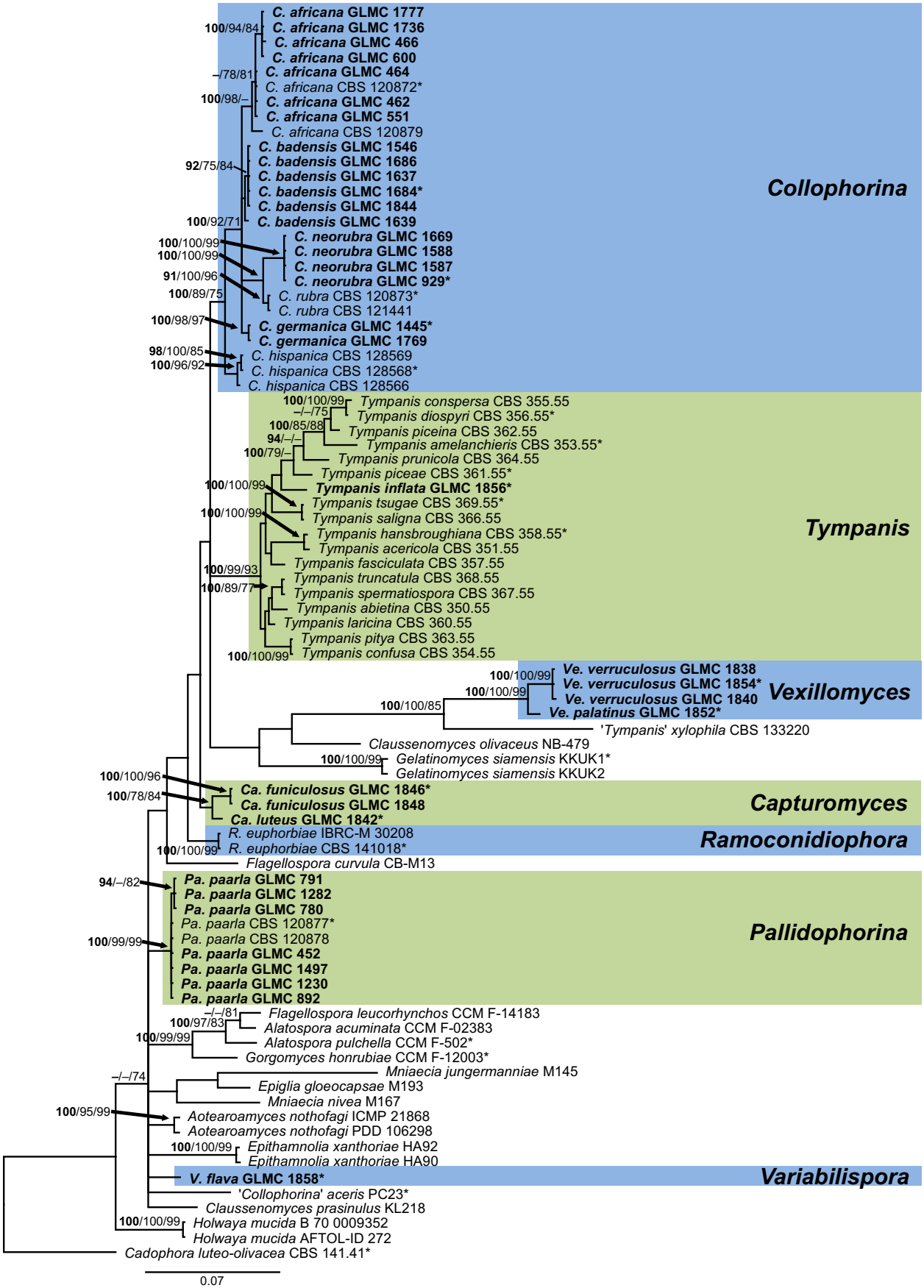

Fig. 1 Phylogeny obtained by bayesian inference analysis of the combined LSU and ITS sequence alignment of species from *Tympanidaceae*. BI posterior probability support values above 90 % (**bold**), ML and MP bootstrap support values above 70 % are shown at the nodes. *Cadophora luteo-olivacea* strain CBS 141.41 is used as outgroup. Numbers of ex-type strains are emphasised with an asterisk (*). Strains analysed in this study are emphasised in **bold**.

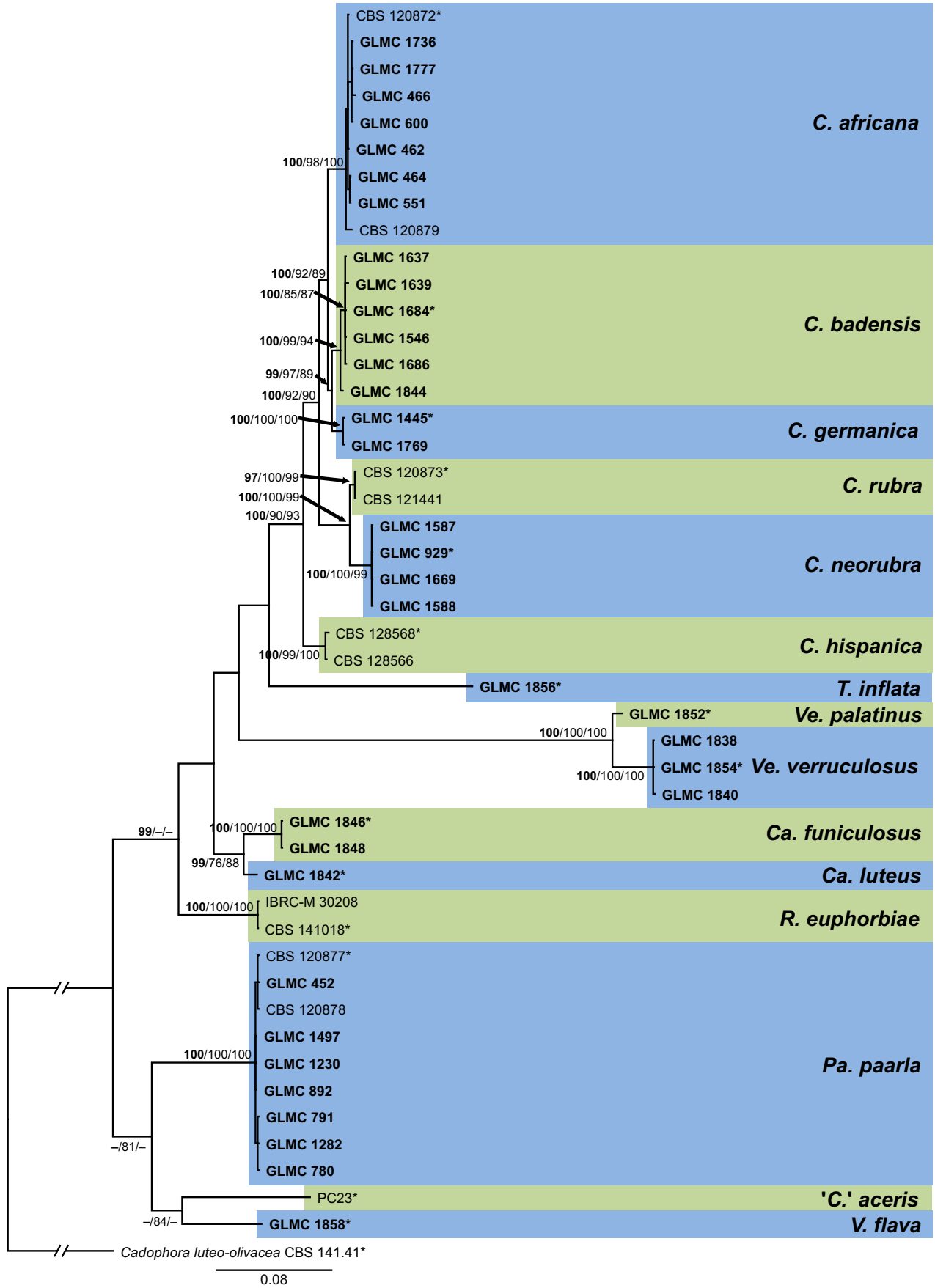

Fig. 2 Phylogeny obtained by bayesian inference analysis of the combined LSU, ITS, *EF-1α*, and *GAPDH* sequence alignment of collophorina-like species. BI posterior probability support values above 90 % (**bold**), ML and MP bootstrap support values above 70 % are shown at the nodes. *Cadophora luteo-olivacea* strain CBS 141.41 is used as outgroup. Numbers of ex-type strains are emphasised with an asterisk (*). Strains analysed in this study are emphasised in **bold**. Branches that are crossed by diagonal lines are shortened by 50 %.

cies based on morphological similarities and blastn searches with the ITS region. One hundred and twelve of the 152 isolates from *Prunus* wood showed a high morphological and sequence similarity with *C. paarla*. The 10 isolates from spore traps and 25 randomly chosen isolates from *Prunus* wood were selected for DNA sequence analyses.

The combined sequence dataset 1 consisted of 84 isolates including the outgroup and comprised 1484 characters, of which 322 characters were parsimony-informative, 425 parsimony-uninformative and 896 constant. The gene boundaries in the multi-locus alignment were as follows: LSU: 1–903, ITS: 904–1484. The most parsimonious tree was generated by MP analysis with tree length: 854 steps, consistency index: 0.423423, retention index: 0.810250 and composite index: 0.385201 and 0.343079 for all sites and parsimony informative sites, respectively. The BI phylogeny obtained by bayesian inference including BI posterior probability values as well as ML (lnL = -8073.184749) and MP bootstrap support values is shown in Fig. 1.

Eighteen strains from *Prunus* wood and one strain from a spore trap (GLMC 1844) isolated in this study form a well-supported clade (100/81/74 % support) together with the ex-type and further strains of the type species of the genus *Collophorina*, *C. rubra*, as well as *C. africana* and *C. hispanica*. This clade consists of six subclades, of which most of them are well-supported. Strain GLMC 1856 isolated from a spore trap integrates in a well-supported clade (100/99/93 % support) of strains of different *Tympanis* species, including one of the type species *T. saligna*. Four strains, GLMC 1838, GLMC 1840, GLMC 1854 and GLMC 1852, isolated from spore traps, form a well-supported clade (100/100/99 % support) next to a strain identified as *Tympanis xylophila* (CBS 133220) which is, however, separated from the *Tympanis* main clade. Strains GLMC 1848, GLMC 1846 and GLMC 1842 isolated from spore traps form a well-supported clade (100/78/84 % support) next to the *C. euphorbiae* clade, including its ex-type strain. A further seven strains from *Prunus* wood form a well-supported clade (100/99/99 % support) with strains of *C. paarla*, including its ex-type strain. Strain GLMC 1858 isolated from spore traps does not integrate into any clade formed by reference strains. Within this phylogeny, previously described species of *Collophorina* do not form a monophyletic clade. A well-supported clade (100/89/75 %) including the type species, *C. rubra*, as well as *C. africana*, *C. hispanica* and three new species recognised in this study is formed excluding *C. aceris*, *C. euphorbiae* and *C. paarla*. Therefore, the genus *Collophorina* is recognised as polyphyletic. The clades, the strains studied in this paper belong to, are consistent in both single LSU and single ITS phylogenies calculated with all three algorithms (BI/ML/MP). Clades consisting only of collophorina-like species are separated by clades formed by strains of *Tympanis*, *Gelatinomyces*, *Aotearoamyces* and strains identified as *Alatospora*, *Epithamnolia*, *Flagellospora*, *Gorgomyces* and *Claussenomyces* spp. No further grouping of the seven main clades consisting of or including collophorina-like species was supported in the LSU-ITS tree.

The combined sequence dataset 2 consisted of 47 isolates including the outgroup and comprised 1829 characters, of which 405 characters were parsimony-informative, 536 parsimony-uninformative and 1202 constant. The gene boundaries in the multi-locus alignment were as follows: LSU: 1–858, ITS: 859–1409, *EF-1α*: 1410–1680, *GAPDH*: 1681–1829. Two most parsimonious trees were generated by MP analysis with tree length: 737 steps, consistency index: 0.639319, retention index: 0.894570, and composite index: 0.611755 and 0.571916 for all sites and parsimony informative sites, respectively. The BI phylogeny obtained by bayesian inference including BI posterior probability values as well as ML (lnL = -7839.866374) and MP bootstrap support values is shown in Fig. 2.

The phylogeny exhibits 15 clades, six of them representing previously defined species. Each seven isolates from necrotic wood of *Prunus* spp. formed well-supported clades with the ex-type strains of *C. africana* and *C. paarla*, respectively (100/98/100 % and 100/100/100 % support). Five isolates from necrotic wood of *P. domestica* sampled in Baden-Württemberg together with an isolate from a spore trap in Rhineland-Palatinate formed a distinct clade (100/99/94 % support), sister to a clade (100/100/100 % support) formed by two isolates from necrotic wood of *P. avium* sampled in Baden-Württemberg and Lower Saxony (GLMC 1445, GLMC 1769), respectively. Four isolates from necrotic wood of *P. avium* sampled in Saxony, Lower Saxony and Baden-Württemberg form a distinct clade (100/100/99 % support), sister to a clade formed by *C. rubra*. Further six distinct clades were formed by isolates from spore traps in Rhineland-Palatinate, two of them by two or three isolates, respectively, and four of them by a single strain each. All single- and multi-locus BI/ML/MP phylogenies showed similar tree typologies.

TAXONOMY

Based on the phylogenetic analyses and sequence comparisons, the strains studied here belong to 11 species in six genera. Nine species that were isolated from necrotic wood of *Prunus* spp. or from spore traps mounted on *Vitis vinifera* vines in Germany were revealed to be new to science and therefore described below. *Collophorina euphorbiae* and *C. paarla* are combined in two newly erected genera, respectively. Further three genera are newly described.

Capturomyces S. Bien, C. Kraus & Damm, *gen. nov.* — MycoBank MB829151

Etymology. Name reflects the way all strains of this genus were retrieved through capture (Lat.: *captura*) of spores with spore traps.

Type species. *Capturomyces funiculosus* S. Bien, C. Kraus & Damm.

Colonies slow-growing, moist, white, buff or yellow colours on oatmeal agar medium, with sparse or lacking aerial mycelium. *Sporulation* conidia formed in conidiomata, on hyphal cells and by microcyclic conidiation. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, intercalary, reduced to discrete phialides, short adelophialides or more often with collarettes formed directly on hyphal cells. *Conidia* aggregated in masses around the hyphae and on the agar surface. *Conidiomata* solitary or aggregated, immersed to superficial, subglobose, uni- to multilocular, dehiscence irregular, appearing cup-shaped when mature. *Conidiophores* hyaline, branched or unbranched, septate. *Conidiogenous cells* enteroblastic, hyaline, conidiogenous loci formed laterally in each cell just below the septum as well as terminally (acropleurogenous). *Conidia* of conidiomata and intercalary hyphal cells small, hyaline, 1-celled, oblong or cylindrical to ellipsoidal, straight or slightly curved.

Capturomyces funiculosus S. Bien, C. Kraus & Damm, *sp. nov.* — MycoBank MB829153; Fig. 3a–b, 4

Etymology. Named after the funiculose mycelium on OA medium.

Typus. Germany, Rhineland-Palatinate, west of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from a spore trap mounted on vine of *V. vinifera*, 17 Mar. 2016, *C. Kraus* (GLM-F112544 holotype; GLMC 1846 = CBS 144840 = DSM 107778 = JKI-Mz50 culture ex-type).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, 1–2.5 µm wide, smooth-walled, lacking

chlamydospores. *Sporulation* abundant, conidia formed on hyphal cells and by microcyclic conidiation. *Conidiophores on hyphae* hyaline, smooth-walled, simple, mostly reduced to conidiogenous cells, directly formed on hyphae, conidiogenous loci formed terminally, 4–10 × 2–3 µm. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, often reduced to mere openings with collarettes formed directly on hyphal cells, adelophialides and discrete phialides, navicular to subcylindrical, often constricted at the base, 3.5–9.5 × 1.5–2 µm; collarettes hardly visible, short tubular, 0.5–1 µm long, opening 1–1.5 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, oblong to ellipsoidal, sometimes slightly curved, with both ends rounded, sometimes with a barely visible scar on one end, 3–5.5(–8.5) × (1–)1.5–2(–2.5) µm, mean ± SD = 4.4 ± 1.2 × 1.7 ± 0.3 µm, L/W ratio = 2.6. *Conidiomata* and *endoconidia* not observed. *Microcyclic conidiation* occurs, from minute collarettes at one or sometimes both ends of primary conidia that develop into swollen mother cells, often thick-walled, sometimes septate, > 5 µm long, 2–3.5 µm wide.

Colonies on OA flat to very low convex with entire to undulate margin, whitish to buff, mycelium on the surface appressed funiculose, aerial mycelium appearing after > 4 wk at the outer margin of the culture, sparse, villose, white to brown; reverse same colours, 8–20 mm diam in 2 wk, 26–36 mm diam in 4 wk; *on SNA* flat with entire to dentate margin, lacking aerial mycelium; whitish to buff; reverse same colours; 8–14 mm diam in 2 wk, 16–28 mm diam in 4 wk.

Additional material examined. Germany, Rhineland-Palatinate, west of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from a spore trap mounted on vine of *V. vinifera*, 17 Mar. 2016, *C. Kraus*, GLM-F112545, culture GLMC 1848 = CBS 144841 = DSM 107779 = JKI-Mz53.

Notes — Isolates of *Capturomyces funiculosus* from spore traps in Rhineland-Palatinate did not produce any pigments on OA medium, similar to '*Collophorina*' *aceris*, *Pallidophorina*

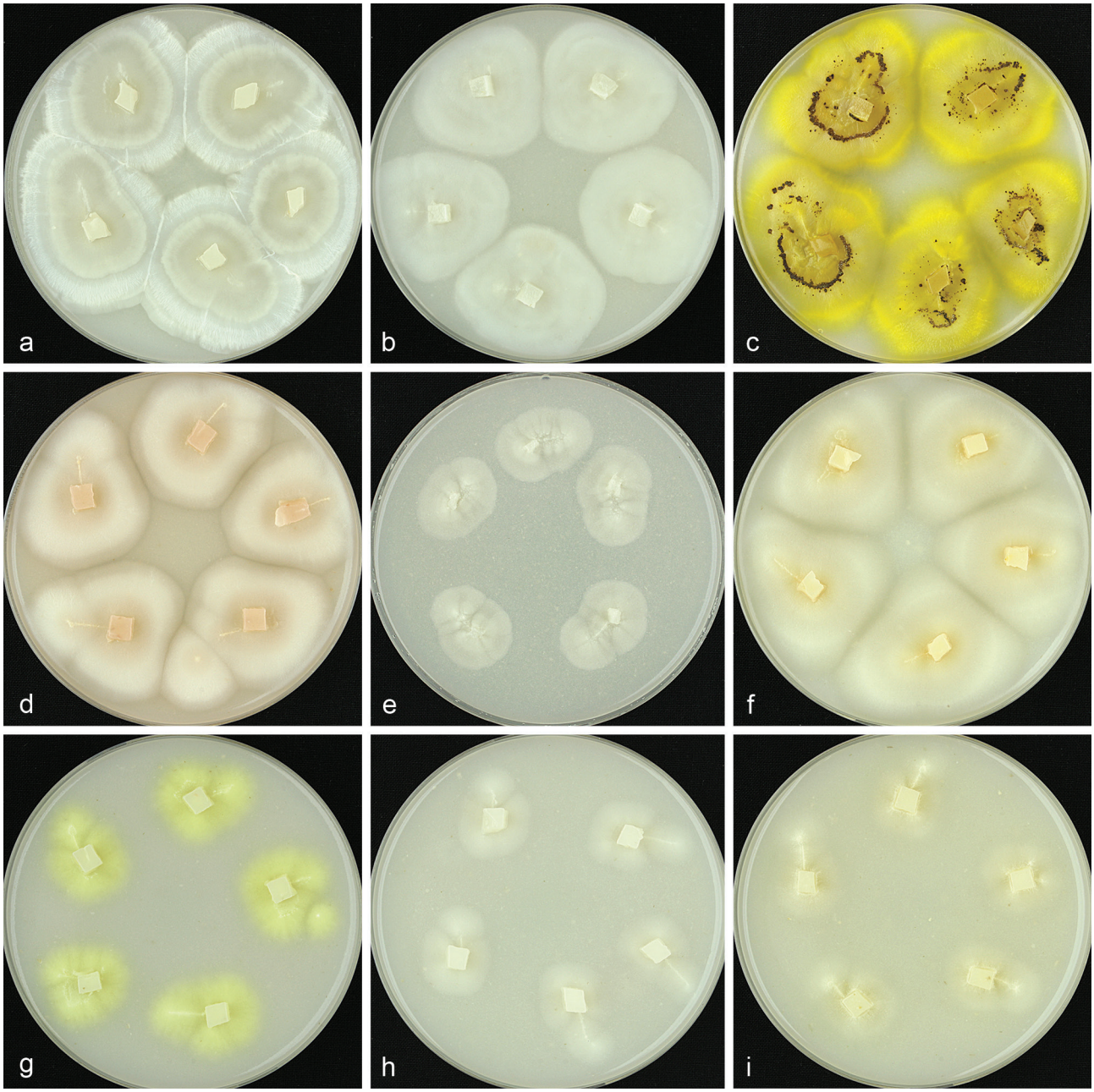

Fig. 3 Colony surface of collophorina-like species on OA medium after 4 wk. a. *Capturomyces funiculosus* GLMC 1848; b. *Ca. funiculosus* GLMC 1846*; c. *Ca. luteus* GLMC 1842*; d. *Pallidophorina paarla* CBS 120877*; e. *Ramoconidiophora euphorbiae* CBS 141018*; f. *Tympanis inflata* GLMC 1856*; g. *Variabilispora flava* GLMC 1858*; h. *Vexillomyces palatinus* GLMC 1852*; i. *Ve. verruculosus* GLMC 1854*. Strains with an asterisk are ex-type cultures.

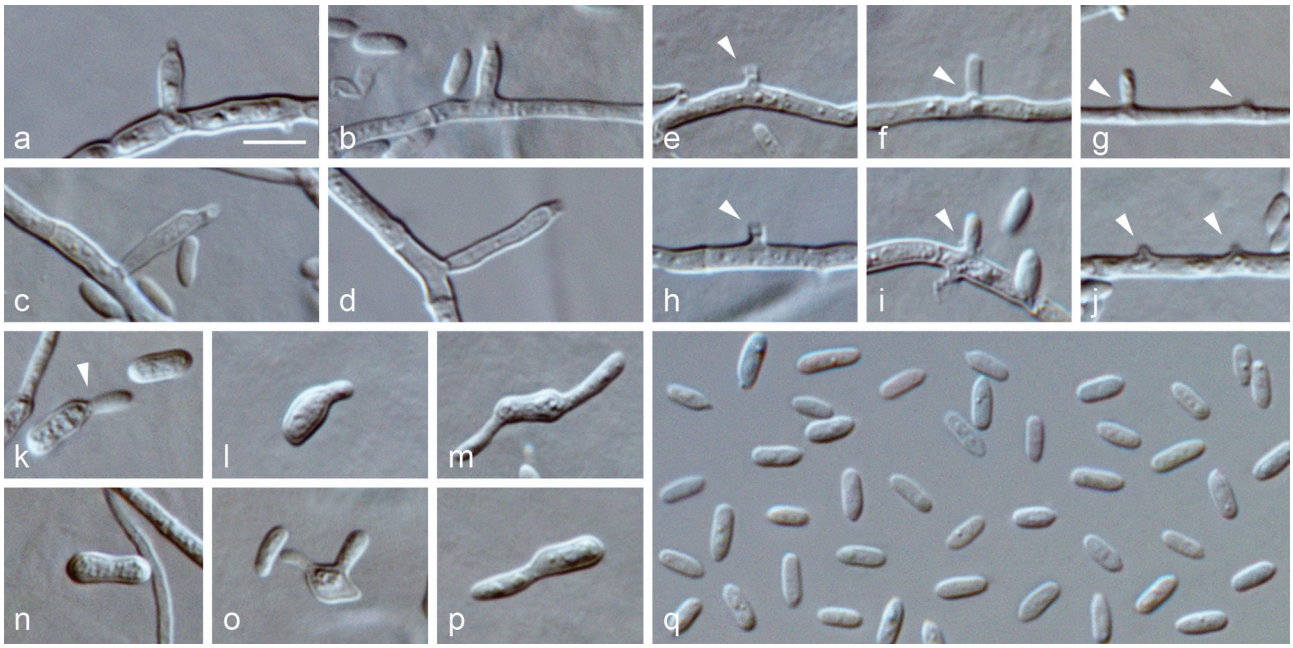

Fig. 4 *Capturomyces funiculosus*. a–j. Conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings or short necks); k–p. mother cells (arrow indicates conidiogenous opening); q. conidia formed on hyphal cells. a–q. From SNA. a–q. LM. — Scale bar: a = 5 µm; scale bar of a applies to b–q.

paarla, *Ramoconidiophora euphorbiae*, *Tympanis inflata*, *Vexillomyces palatinus* and *Ve. verruculosus*. The closest relative is *Capturomyces luteus* with one, 13, 22 and 11 nucleotide differences in the LSU, ITS, *EF-1α* and *GAPDH* sequences, respectively. In contrast to *Ca. luteus*, *Ca. funiculosus* lacks a yellow pigment in OA cultures and conidiomata were not observed. In a blastn search in GenBank, the ITS sequence of *Ca. funiculosus* showed 100 % identity with an unidentified ascomycete from a stump of *Picea abies* in Finland (MG190490, 92 % coverage, J Kaitera & HM Henttonen unpubl. data) and a *Leotiomycetes* sp. from bark tissue of *Tsuga canadensis* in Canada (KX589233, 90 % coverage, KM Complak et al. unpubl. data).

Capturomyces luteus S. Bien, C. Kraus & Damm, *sp. nov.* — MycoBank MB829154; Fig. 3c, 5

Etymology. Named after its luteous colonies on OA medium.

Typus. Germany, Rhineland-Palatinate, west of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from a spore trap mounted on vine of *V. vinifera*, 6 May 2016, *C. Kraus* (GLM-F112542 holotype; GLMC 1842 = CBS 144839 = DSM 107780 = JKI-Mai12 culture ex-type).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled, lacking chlamydospores, 1–2.5 µm wide. *Sporulation* abundant, conidia formed directly on hyphal cells, in conidiomata and by microcyclic conidiation. *Conidiophores on hyphae* hyaline, smooth-walled, simple, constricted at the base, conidiogenous loci formed terminally, mostly reduced to conidiogenous cells, directly formed on hyphae. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, mostly reduced to mere openings with collarettes or short necks formed directly on hyphal cells, discrete phialides and adelophialides rarely observed, subcylindrical to navicular, constricted at the base, 4–6 × 2 µm; necks short, cylindrical, 1–1.5 × 1–1.5 µm; collarettes rarely visible, tubular, 0.5–1 µm long, opening 0.5–1.5 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, oblong to ellipsoidal, mostly straight, sometimes slightly curved, with both ends rounded, sometimes with a prominent scar on one end, 3–5.5(–7) × 1.5–2(–2.5) µm, mean ± SD = 4.3 ± 1.1 × 1.7 ± 0.3 µm, L/W ratio = 2.5. *Conidiomata* produced on pine needles, on OA and on SNA in > 4 wk; solitary or aggregated, subglobose, uni- to multilocular, immersed to superficial, 60–400 µm wide, light brown to dark brown, sometimes nearly glabrous, but mostly densely covered with hairs, opening with an irregular rupture, often showing a light-coloured inner part with a darker, central dot or elongated stripe. *Conidiophores* hyaline, smooth-walled, septate, sometimes branched at the base and above, straight or slightly zigzag-shaped, often constricted at the septa, 10–35 µm long, conidiogenous loci formed terminally as well as intercalary, immediately below the septum. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, 5–7.5 × 1.5–2.5 µm; collarettes tubular, often inconspicuous, < 0.5–1 µm long, opening 0.5–1 µm, periclinal thickening sometimes visible. *Conidia* hyaline, smooth-walled, cylindrical to ellipsoidal, sometimes slightly curved, with both ends rounded, 3–4(–4.5) × 1.5–2 µm, mean ± SD = 3.6 ± 0.4 × 1.6 ± 0.1 µm, L/W ratio = 2.3. *Endoconidia* not observed. *Microcyclic conidiation* occurs from minute collarettes at one or both ends of primary conidia that develop into swollen mother cells, often thick-walled, sometimes septate, > 5 µm long, 3–4 µm wide.

Colonies on OA flat to very low convex with entire to undulate margin, lacking aerial mycelium; buff, with scattered sienna to umber spots due to conidiomata formation, spore mass oozing from conidiomata buff, after > 4 wk colony pale luteous, luteous to amber; reverse same colours, 16–20 mm diam in 2 wk, 26–34 mm diam in 4 wk; *on SNA* flat with fimbriate to rhizoid margin, lacking aerial mycelium; initially white, after > 4 wk with fulvous to sienna spots due to conidiomata formation; reverse same colours; 6–10 mm diam in 2 wk, 12–16 mm diam in 4 wk.

Notes — *Capturomyces luteus* differs from all other species of collophorina-like fungi by a luteous pigment formed in OA cultures. The closest relative is *Ca. funiculosus* with one, 13, 22 and 11 nucleotide differences in the LSU, ITS, *EF-1α* and the partly generated *GAPDH* sequence (only the second half of the *GAPDH* sequence is available), respectively. Although morphologically similar, *Ca. luteus* can be easily differentiated from *Ca. funiculosus* by the yellow pigment produced on OA as well as by the abundant development of conidiomata. In a blastn search in GenBank, the ITS sequence of *Ca. luteus* showed 100 % identity with strains (HM240822, 89 % cover-

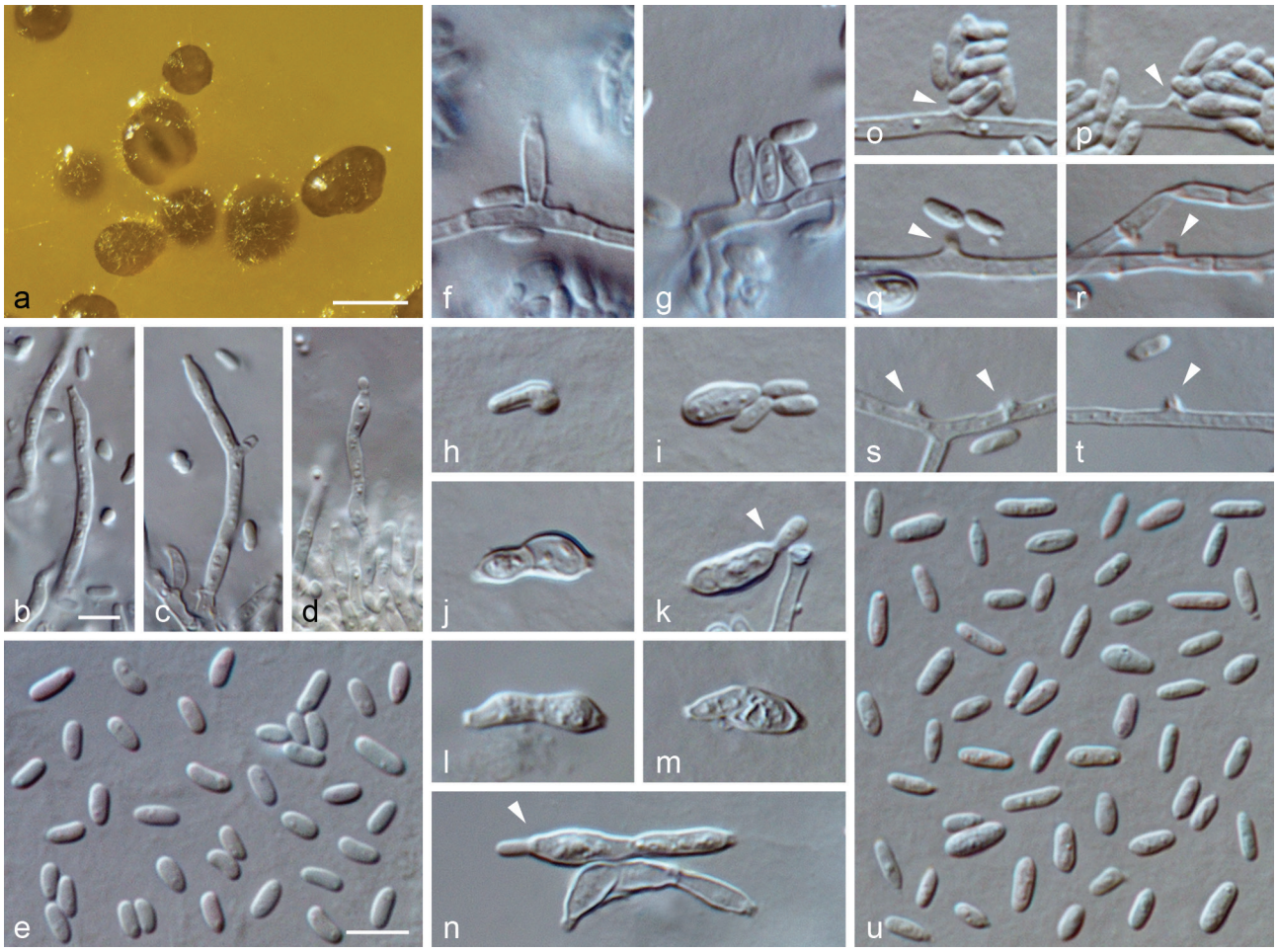

Fig. 5 *Capturomyces luteus*. a. Conidiomata; b–d. conidiogenous cells lining the inner wall of a conidioma; e. conidia formed in conidiomata; f–g, o–t. conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings or short necks); h–n. mother cells (arrows indicate microcyclic conidiation); u. conidia formed on hyphal cells. a–e. From OA; f–u. from SNA. a. SM; b–u. LM. — Scale bars: a = 300 µm, b, e = 5 µm; scale bar of b applies to c–d, scale bar of e applies to f–u.

age; MG190551, 92 % coverage,) isolated from a needle and a stump, respectively, of *Pinus sylvestris* in Finland (Terhonen et al. 2011; J Kaitera & HM Henttonen unpubl. data). An isolate from healthy twigs of *P. sylvestris* in Spain (JX421713) showed a 99 % identity (4 nucleotide differences, 95 % coverage, Sanz-Ros et al. 2015).

Collophorina africana (Damm & Crous) Damm & Crous, Fungal Diversity 86: 111. 2017; Fig. 6a

Basionym. *Collophora africana* Damm & Crous, Persoonia 24: 65. 2010.
Synonym. *Collophora capensis* Damm & Crous, Persoonia 24: 67. 2010.

Typus. South Africa, Western Cape Province, Paarl, from reddish brown necrosis in wood of *P. salicina*, 10 June 2004, *U. Damm* (CBS H-19993 holotype; CBS 120872 = STE-U 6113 = GLMC 1882 culture ex-type).

A description is provided in Damm et al. (2010).

Additional materials examined. Germany, Baden-Württemberg, in orchard south of Oppenau, N48°27'58.4" E8°09'26.7", from brown wedge-shaped necrosis in wood of *P. domestica*, 24 Aug. 2016, *S. Bien*, GLM-F110819, culture GLMC 1736 = CBS 144835 = DSM 107849; Baden-Württemberg, in orchard south of Oppenau, N48°27'58.4" E8°09'26.7", from brown wedge-shaped necrosis in wood of *P. domestica*, 24 Aug. 2016, *S. Bien*, GLM-F110860, culture GLMC 1777 = CBS 144837 = DSM 107850; Saxony, in orchard north of Wölkau, N50°58'42.3" E13°49'40.0", from brown wedge-shaped necrosis in wood of *P. domestica*, 2 Mar. 2016, *S. Bien*, GLM-F106312, culture GLMC 462; Saxony, in orchard north of Wölkau, N50°58'42.3" E13°49'40.0", from brown wedge-shaped necrosis in wood of *P. domestica*, 2 Mar. 2016, *S. Bien*, GLM-F106314, culture GLMC 464; Saxony, in orchard north of Wölkau, N50°58'42.3" E13°49'40.0", from brown wedge-shaped necrosis in wood of *P. domestica*, 2 Mar. 2016, *S. Bien*, GLM-F106316, culture GLMC 466; Saxony, in orchard north of Wölkau, N50°58'42.3" E13°49'40.0", from brown wedge-shaped necrosis in wood of *P. domestica*, 2 Mar. 2016, *S. Bien*, GLM-F106401, culture GLMC 551; Saxony, in orchard north of Wölkau, N50°58'42.3" E13°49'40.0", from brown wedge-shaped necrosis in wood of *P. domestica*, 2 Mar. 2016, *S. Bien*, GLM-F106450, culture GLMC 600.

Notes — *Collophorina africana* was isolated seven and 14 times from wood of *P. domestica* in Saxony and Baden-Württemberg, respectively. It was not found in spore traps.

Collophorina badensis S. Bien & Damm, *sp. nov.* — MycoBank MB829147; Fig. 6b, 7

Etymology. Named after the geographical region in southern Germany, in which most isolates including the ex-type strain were isolated.

Typus. Germany, Baden-Württemberg, orchard west of Nussbach, N48°31'55.8" E8°00'52.4", from non-symptomatic wood of *P. domestica*, 23 Aug. 2016, *S. Bien* (GLM-F110767 holotype; GLMC 1684 = CBS 144833 = DSM 107769 culture ex-type).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled, 1.5–3 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed on hyphal cells, in conidiomata and by microcyclic conidiation. *Conidiophores on hyphae* hyaline, smooth-walled, simple or septate, 3–30 µm long, mostly reduced to conidiogenous cells, directly formed on hyphae, conidiogenous loci formed terminally and sometimes intercalary, immediately below the septum. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, 3–9 × 1.5–3 µm, often reduced to mere openings formed directly on hyphal cells, discrete phialides or adelophialides, ampulli-

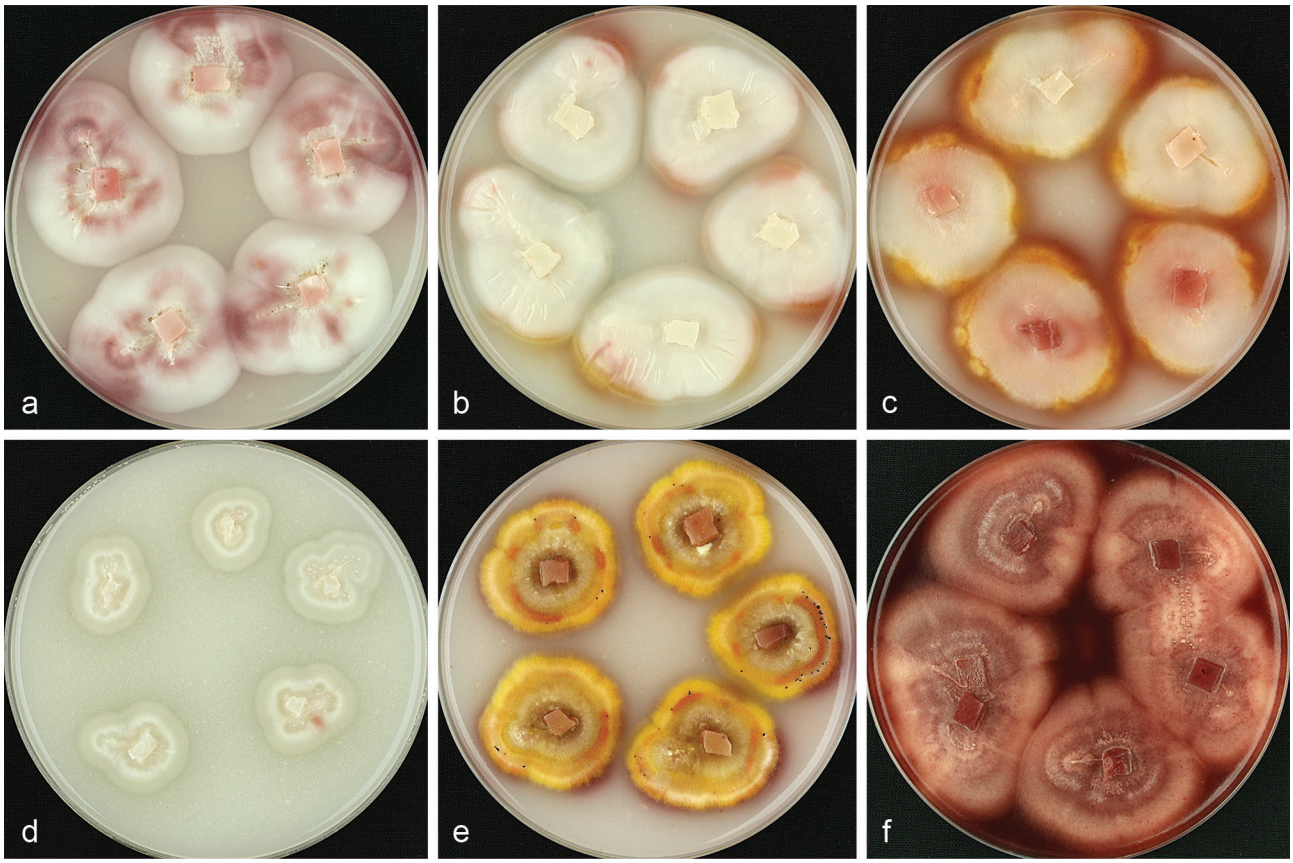

Fig. 6 Colony surface of *Collophorina* species on OA medium after 4 wk. a. *Collophorina africana* CBS 120872*; b. *C. badensis* GLMC 1684*; c. *C. germanica* GLMC 1445*; d. *C. hispanica* CBS 128568*; e. *C. neorubra* GLMC 929*; f. *C. rubra* CBS 120873*. Strains with an asterisk are ex-type cultures.

form to navicular, sometimes reduced to short necks, with short tubular to funnel-shaped collarettes, opening 0.5–1.5 µm diam, collarettes minute, < 0.5 µm long, opening 0.5–1.5 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, cylindrical to oblong, mostly straight, sometimes slightly curved, with obtuse ends, sometimes with a barely visible scar on one end, (3–)3.5–5.5(–6) × 1.5–2(–2.5) µm, mean ± SD = 4.4 ± 0.9 × 1.8 ± 0.3 µm, L/W ratio = 2.4. *Conidiomata* produced on OA in 2–4 wk, solitary or aggregated, subglobose, uni- to multilocular, immersed to erumpent, 50–300 µm wide, after > 4 wk up to 700 µm wide, light to dark brown, opening with an irregular rupture. *Conidiophores* hyaline, smooth-walled, straight, septate, often constricted at the septa, sometimes branched at the base and above, conidiogenous loci formed intercalary, immediately below the septum as well as terminally, 10–30 µm long. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, 4.5–8.5 × 2–2.5 µm; collarettes cylindrical, often inconspicuous, < 1 µm long, opening 0.5–1 µm, periclinal thickening sometimes visible. *Conidia* hyaline, after > 4 wk some of the conidia become reddish, smooth-walled, cylindrical to ellipsoidal, with both ends rounded, sometimes slightly curved, (2–)2.5–4(–5) × 1–2 µm, mean ± SD = 3.4 ± 0.7 × 1.5 ± 0.3 µm, L/W ratio = 2.3. *Endoconidia* not observed. *Microcyclic conidiation* occurs from minute collarettes at one or rarely both ends of primary conidia that develop into swollen mother cells, often thick-walled, sometimes septate, > 5 µm long, 2–4.5 µm wide. *Colonies on OA* flat to very low convex with entire margin; initially buff, sometimes with cinnamon to black spots due to conidiomata, after > 4 wk colony turning scarlet to bay, reddish pigment released into surrounding medium, spore mass from conidiomata pale luteous, after > 4 wk turning to blood colour; aerial mycelium sparse, white; reverse same colours; 6–12 mm diam in 2 wk, 20–32 mm diam in 4 wk; *on SNA* flat to very low convex with entire to undulate margin, whitish; lacking aerial mycelium; reverse same colours; 8–12 mm diam in 2 wk, 18–26 mm diam in 4 wk.

Additional materials examined. Germany, Baden-Württemberg, orchard west of Nussbach, N48°31'55.8" E8°00'52.4", from brown wedge-shaped necrosis in wood of *P. domestica*, 23 Aug. 2016, *S. Bien*, GLM-F110769, culture GLMC 1686 = CBS 144834 = DSM 107770; Baden-Württemberg, orchard east of Nussbach, N48°31'57.3" E8°01'49.6", from brown wedge-shaped necrosis in wood of *P. domestica*, 23 Aug. 2016, *S. Bien*, GLM-F110626, culture GLMC 1546; Baden-Württemberg, orchard west of Nussbach, N48°31'55.8" E8°00'52.4", from brown wedge-shaped necrosis in wood of *P. domestica*, 23 Aug. 2016, *S. Bien*, GLM-F110717, culture GLMC 1637; Baden-Württemberg, orchard west of Nussbach, N48°31'55.8" E8°00'52.4", from brown wedge-shaped necrosis in wood of *P. domestica*, 23 Aug. 2016, *S. Bien*, GLM-F110719, culture GLMC 1639; Rhineland-Palatinate, west of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from a spore trap mounted on vine of *V. vinifera*, 25 May 2016, *C. Kraus*, GLM-F112543, culture GLMC 1844 = JKI-Mai59.

Notes — *Collophorina badensis* produces a red pigment like *C. africana*, *C. germanica*, *C. hispanica*, *C. neorubra* and *C. rubra*. The species is closely related to *C. germanica* with at least two, five, nine and four nucleotide differences in the LSU, ITS, *EF-1α* and *GAPDH* sequences, respectively. Conidia of *C. badensis* produced on hyphae and by microcyclic conidiation are less often curved than those of *C. germanica*. Strains of this species were almost exclusively isolated from *P. domestica* in Baden-Württemberg, while *C. germanica* is so far only known from wood of *P. avium*. One strain was isolated from a spore trap in Rhineland-Palatinate. The *EF-1α* sequence of this isolate differs in five nucleotides from that of the other isolates, while the LSU, ITS and the *GAPDH* sequences are identical.

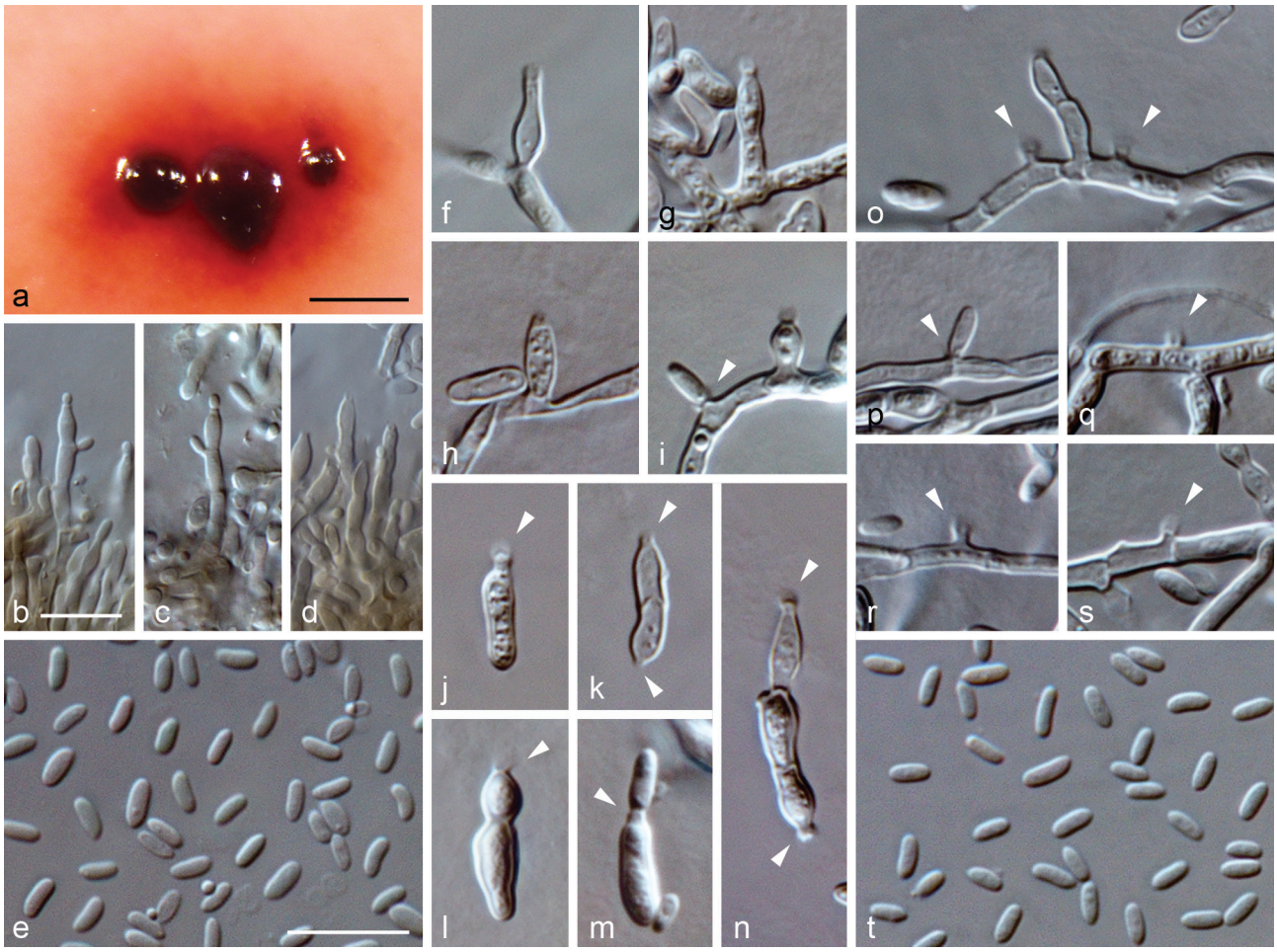

Fig. 7 *Collophorina badensis*. a. Conidiomata; b–d. conidiogenous cells lining the inner wall of a conidioma; e. conidia formed in conidiomata; f–i, o–s. conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings or short necks); j–n. mother cells (arrows indicate conidiogenous openings); t. conidia formed on hyphal cells. a–e. From OA; f–t. from SNA. a. SM; b–t. LM. — Scale bars: a = 400 µm, b, e = 10 µm; scale bar of b applies to c–d, scale bar of e applies to f–t.

Collophorina germanica S. Bien & Damm, *sp. nov.* — MycoBank MB829148; Fig. 6c, 8

Etymology. Named after the country of isolation.

Typus. Germany, Lower-Saxony, Hollern-Twielenfleth, orchard, N53°35'16.1" E9°34'23.7", from brown necrosis in wood of *P. avium*, 8 Oct. 2015, *S. Bien* (GLM-F110545 holotype; GLMC 1445 = CBS 144831 = DSM 107771 culture ex-type).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled, 1–3.5 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed on hyphal cells, in conidiomata and by microcyclic conidiation. *Conidiophores on hyphae* hyaline, smooth-walled, simple or septate, mostly reduced to conidiogenous cells, directly formed on hyphae, conidiogenous loci formed terminally and sometimes intercalary, immediately below the septum, 3–30 µm long. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, often reduced to mere openings formed directly on hyphal cells, discrete phialides ampulliform to navicular, sometimes reduced to short necks, 2.5–10 × 2–2.5 µm, collarettes tubular to funnel-shaped, < 0.5–1 µm long, opening 1–1.5 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, oblong to allantoid, rarely sigmoid, with obtuse ends, 4–8.5(–12) × 1.5–2(–2.5) µm, mean ± SD = 6.1 ± 2.3 × 1.8 ± 0.2 µm, L/W ratio = 3.4. *Conidiomata* produced on OA, rarely on SNA, in 4–8 wk; solitary or aggregated, subglobose, uni- to multilocular, immersed to superficial, 80–230 µm wide, dark brown to black, nearly glabrous to completely covered with hairs, opening with an irregular rupture. *Conidiophores* hyaline, smooth-walled, septate, constricted at the septa, straight, sometimes branched at the base and above, often not terminating in phialides, but with sterile, mostly pointed, sometimes inflated cells, 10–30 µm long, conidiogenous loci formed terminally or rarely intercalary, immediately below the septum. *Conidiogenous cells*, enteroblastic, hyaline, smooth-walled, 4–7 × 2–3 µm, collarettes cylindrical, often inconspicuous, < 1 µm long, opening 0.5–1.5 µm, periclinal thickening sometimes visible. *Conidia* hyaline to very pale brown, smooth-walled, cylindrical to ellipsoidal, with both ends rounded, 2.5–3.5 × (1–)1.5–2 µm, mean ± SD = 3 ± 0.3 × 1.6 ± 0.1 µm, L/W ratio = 1.9. *Endoconidia* not observed. *Microcyclic conidiation* occurs from minute collarettes at one or sometimes both ends of primary conidia that develop into swollen mother cells, often thick-walled, sometimes septate, > 6 µm long, 2.5–3.5 µm wide.

Colonies on OA flat to very low convex with entire to undulate margin; aerial mycelium not observed, buff to pale luteous in the centre, apricot to scarlet towards the margin, with black spots due to conidiomata formation, conidiomata oozing buff spore mass, reddish pigment released into surrounding medium, after > 4 wk whole colony becoming darker (up to bay); reverse same colours, 12–20 mm diam in 2 wk, 22–32 mm diam in 4 wk; *on SNA* flat to very low convex with entire, undulate, dentate or fimbriate margin, lacking aerial mycelium, white to luteous; reverse same colours; 10–12 mm diam in 2 wk, 12–22 mm diam in 4 wk.

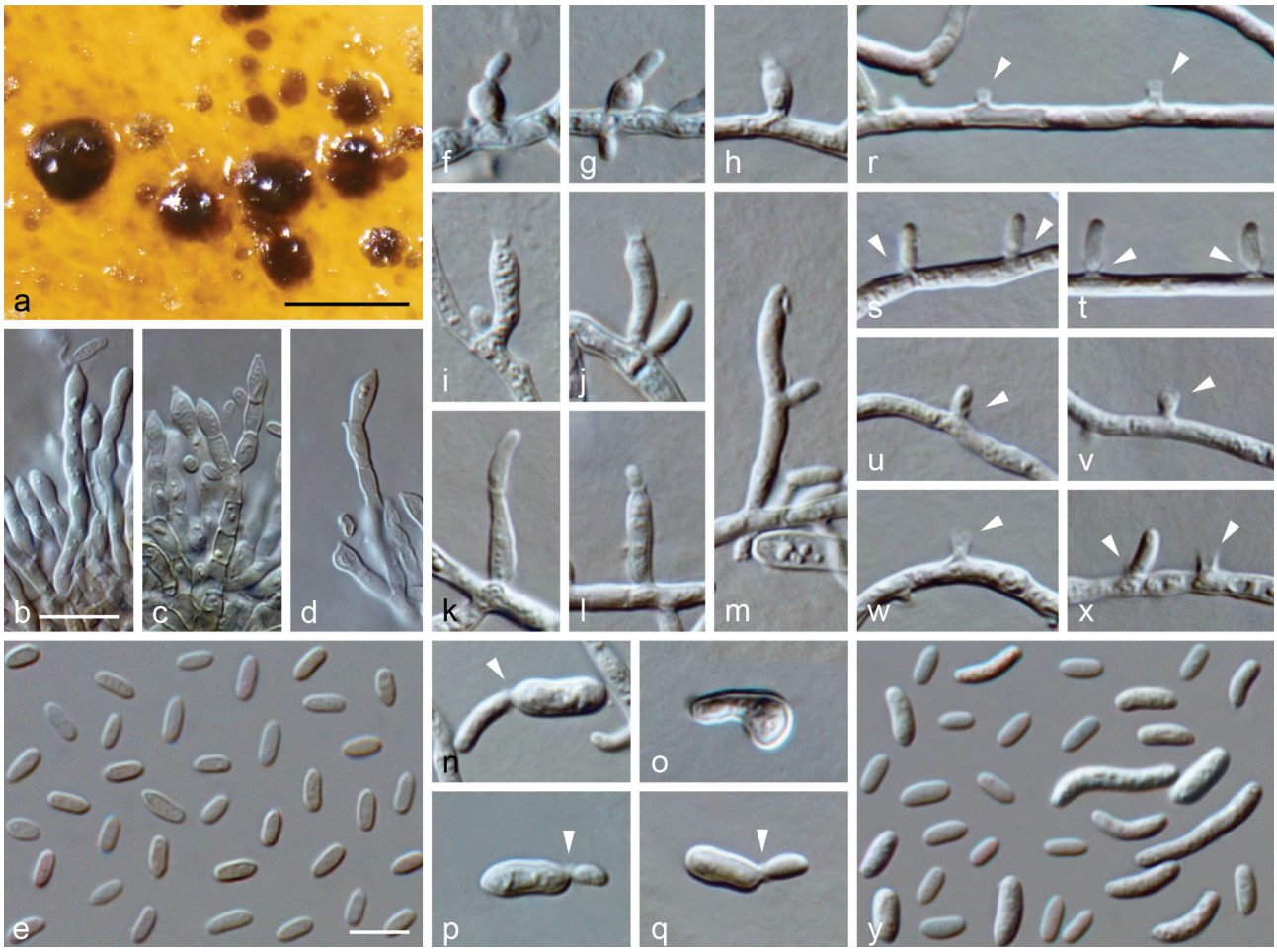

Fig. 8 *Collophorina germanica*. a. Conidiomata; b–d. conidiogenous cells lining the inner wall of a conidioma; e. conidia formed in conidiomata; f–m, r–x. conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings or short necks); n–q. mother cells (arrows indicate conidiogenous openings); y. conidia formed on hyphal cells. a–e. From OA; f–y. from SNA. a. SM; b–y. LM. — Scale bars: a = 300 µm, b = 10 µm, e = 5 µm; scale bar of b applies to c–d, scale bar of e applies to f–y.

Additional material examined. Germany, Baden-Württemberg, orchard south of Oppenau, on hill, N48°27'57.6" E8°09'11.0", from brown necrosis in wood of *P. avium*, 24 Aug. 2016, *S. Bien*, GLM-F110852, culture GLMC 1769 = CBS 144836 = DSM 107772.

Notes — *Collophorina germanica* produces a red pigment like *C. africana*, *C. badensis*, *C. hispanica*, *C. neorubra* and *C. rubra*. The closest relative is *C. badensis* with two, five, nine and four nucleotide differences in the LSU, ITS, *EF-1α* and *GAPDH* sequences, respectively. However, conidia produced on hyphae are more often allantoid to sigmoid than those of *C. badensis*. The two isolates originate from necrotic wood of *P. avium* in the most northern and most southern sampling areas in Germany.

Collophorina neorubra S. Bien & Damm, *sp. nov.* — MycoBank MB829149; Fig. 6e, 9

Etymology. Named based on the closest relative, *C. rubra*.

Typus. Germany, Saxony, orchard east of Gombson, N50°57'17.6" E13°47'19.3", from dark brown necrosis in wood of *P. avium*, 11 Aug. 2015, *S. Bien* (GLM-F106779 holotype; GLMC 929 = CBS 144829 = DSM 107773 culture ex-type).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled, 1.5–3.5 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed directly on hyphal cells, in conidiomata and by microcyclic conidiation. *Conidiophores on hyphae* hyaline, smooth-walled, simple or septate, conidiogenous loci formed terminally and sometimes intercalary, immediately below the septum, mostly reduced to conidiogenous cells, directly formed on hyphae, 3–30 µm long. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, often reduced to mere openings formed directly on hyphal cells, discrete phialides, ampulliform to navicular, 3–8 × 2–3 µm, collarettes tubular to funnel-shaped, 0.5–1.5 µm long, opening < 1–1.5 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, oblong to ellipsoid, sometimes slightly curved, with obtuse ends, (3–)3.5–5(–7) × (1–)1.5–2.5 µm, mean ± SD = 4.3 ± 0.8 × 1.8 ± 0.5 µm, L/W ratio = 2.4. *Conidiomata* produced on OA in 2–4 wk; solitary or aggregated, uni- to multilocular, immersed to superficial, light to dark brown, subglobose, nearly glabrous to completely covered with hyaline to brown hairs, 100–600 µm wide, opening with an irregular rupture. *Conidiophores* hyaline, smooth-walled, septate, sometimes branched at the base and above, straight or slightly zigzag-shaped, often constricted at the septa, 10–30 µm long, conidiogenous loci formed intercalary, immediately below the septum as well as terminally. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, 5–7.5 × 1.5–2.5 µm, collarettes cylindrical, short, often inconspicuous, 0.5–1 µm long, opening 0.5–1 µm, periclinal thickening sometimes visible. *Conidia* hyaline, later turning to pale red, smooth-walled, cylindrical to ellipsoidal, sometimes slightly curved, with both ends rounded, 3–4(–4.5) × 1–1.5 µm, mean ± SD = 3.4 ± 0.4 × 1.5 ± 0.1 µm, L/W ratio = 2.3. *Endoconidia* not observed. *Microcyclic conidiation* occurs from minute collarettes at one or both ends of primary conidia that develop into swollen mother cells, often thick-walled, sometimes septate,

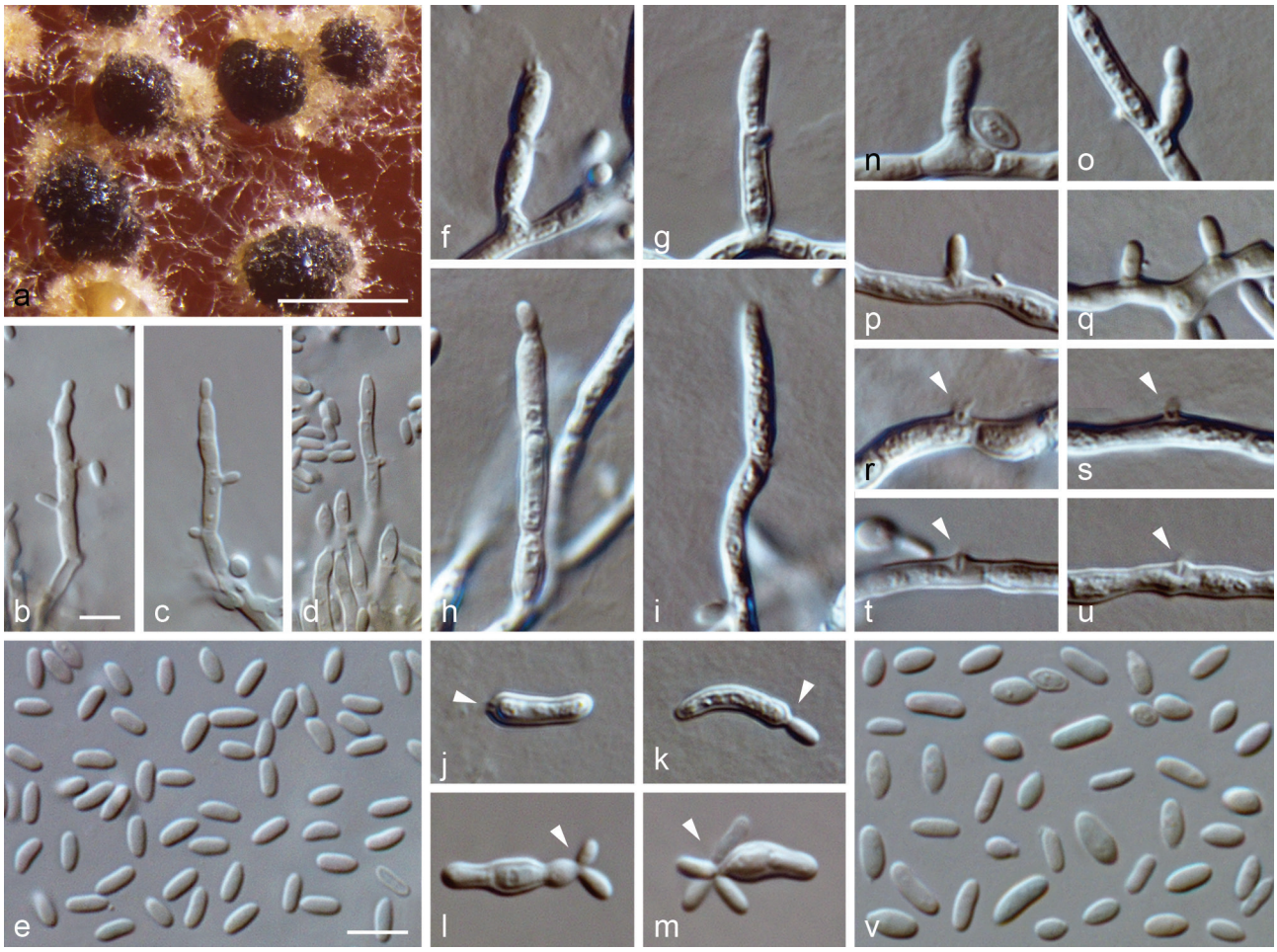

Fig. 9 *Collophorina neorubra*. a. Conidiomata; b–d. conidiogenous cells lining the inner wall of a conidioma; e. conidia formed in conidiomata; f–i, n–u. conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings); j–m. mother cells (arrows indicate conidiogenous openings); v. conidia formed on hyphal cells. a–e. From OA; f–v. from SNA. a. SM; b–v. LM. — Scale bars: a = 300 µm, b, e = 5 µm; scale bar of b applies to c–d, scale bar of e applies to f–v.

> 5 µm long, 2–3.5 µm wide, often more than one conidium attached to an opening.

Colonies on OA flat to very low convex with entire to undulate margin, pale luteous to luteous, apricot to orange, margin white; with saffron to black spots due to conidiomata formation, spore mass pale oozing from conidiomata luteous to bay, reddish pigment released into surrounding medium, aerial mycelium sparse, white, after > 4 wk colony turning to bay; reverse same colours; 12–16 mm diam in 2 wk, 20–24 mm diam in 4 wk; *on SNA* flat to very low convex with entire, undulate, dentate to fimbriate margin, lacking aerial mycelium; white to luteous; reverse same colours; < 1–2 mm diam in 2 wk, < 1–2 mm diam in 4 wk.

Additional materials examined. Germany, Baden-Württemberg, orchard west of Nussbach, N48°32'11.3" E8°01'01.3", from brown necrosis in wood of *P. avium*, 23 Aug. 2016, *S. Bien*, GLM-F110752, culture GLMC 1669 = CBS 144832 = DSM 107774; Lower-Saxony, Hollern-Twielenfleth, orchard, N53°35'16.1" E9°34'23.7", from brown necrosis in wood of *P. avium*, 8 Oct. 2015, *S. Bien*, GLM-F110667, culture GLMC 1587; Lower-Saxony, Hollern-Twielenfleth, orchard, N53°35'16.1" E9°34'23.7", from brown necrosis in wood of *P. avium*, 8 Oct. 2015, *S. Bien*, GLM-F110668, culture GLMC 1588.

Notes — *Collophorina neorubra* is closely related to *C. rubra* with nine, four, two and seven nucleotide differences in the LSU, ITS, *EF-1α* and *GAPDH* sequences, respectively. It produces a red pigment like *C. africana*, *C. badensis*, *C. germanica*, *C. hispanica* and *C. rubra*. Damm et al. (2010) described the phialides of the closely related *C. rubra* as particularly short with a maximum of 4 µm in length. However, up to 8 µm long phialides were observed in *C. neorubra*. A unique feature of this species is the frequent attachment of two to several conidia at the conidiogenous openings of the mother cells during microcyclic conidiation. *Collophorina neorubra* has only been isolated from wood of *P. avium*, but in all the production areas sampled, Baden-Württemberg, Saxony and Lower Saxony.

Pallidophorina S. Bien & Damm, *gen. nov.* — MycoBank MB829160

Etymology. Name refers to the pale (Lat.: *pallidus*) appearance of the culture on oatmeal agar medium and the resemblance to *Collophorina*.

Type species. *Pallidophorina paarla* (Damm & Crous) S. Bien & Damm.

Colonies slow-growing, moist, white or cream colours on oatmeal agar medium, with sparse or lacking aerial mycelium. *Sporulation* conidia formed in conidiomata, on hyphal cells and by microcyclic conidiation. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, intercalary, reduced to short adelophialides, discrete phialides or more often to openings with collarettes formed directly on hyphal cells. *Conidia* aggregated in masses around the hyphae and on the agar surface. *Conidiomata* solitary or aggregated, subglobose, superficial or semi-immersed, uni- to multilocular, dehiscence irregular. *Conidiophores* hyaline, simple or branched, septate, filiform. *Conidiogenous cells* enteroblastic, hyaline, often short necks formed laterally in each cell just below the septum as well as terminally (acropleurogenous). *Conidia* of conidiomata and intercalary hyphal cells small, hyaline, 1-celled, cylindrical to ellipsoidal.

Pallidophorina paarla (Damm & Crous) S. Bien & Damm, *comb. nov*. — MycoBank MB829162; Fig. 3d

Basionym. *Collophora paarla* Damm & Crous, Persoonia 24: 67. 2010.
Synonyms. *Collophora pallida* Damm & Crous, Persoonia 24: 69. 2010.
Collophorina paarla (Damm & Crous) Damm & Crous, Fungal Diversity 86: 111. 2017.

Typus. South Africa, Western Cape Province, Paarl, from dark brown necrosis in wood of *P. persica*, 10 June 2004, *U. Damm* (CBS H-19996 holotype; CBS 120877 = STE-U 6114 = GLMC 1884 culture ex-type).

A description is provided in Damm et al. (2010).

Additional materials examined. Germany, Saxony, orchard north of Kunnerwitz, N51°07'27.5" E14°56'36.3", from dark brown necrosis in wood of *P. cerasus*, 15 Jan. 2015, *S. Bien*, GLM-F106302, culture GLMC 452 = CBS 144828 = DSM 107775; Lower-Saxony, orchard in Hollern-Twielenfleth, N53°36'13.6" E9°31'50.8", from brown necrosis in wood of *P. domestica*, 8 Oct. 2015, *S. Bien*, GLM-F107132, culture GLMC 1282 = CBS 144830 = DSM 107776; Saxony, orchard east of Borthen, N50°58'20.9" E13°48'48.1", from dark brown necrosis in wood of *P. domestica*, 11 Aug. 2015, *S. Bien*, GLM-F106630, culture GLMC 780; Saxony, orchard east of Lungkwitz, N50°56'12.4" E13°47'36.6", from dark brown necrosis in wood of *P. cerasus*, 11 Aug. 2015, *S. Bien*, GLM-F106641, culture GLMC 791; Saxony, orchard east of Gombson, N50°57'19.3" E13°47'22.0", from dark brown necrosis in wood of *P. avium*, 11 Aug. 2015, *S. Bien*, GLM-F106742, culture GLMC 892; Lower-Saxony, orchard in Hollern-Twielenfleth, N53°36'13.6" E9°31'50.8", from brown necrosis in wood of *P. avium*, 8 Oct. 2015, *S. Bien*, GLM-F107080, culture GLMC 1230; Baden-Württemberg, orchard east of Erlach, N48°34'17.3" E8°02'13.6", from brown necrosis in wood of *P. avium*, 23 Aug. 2016, *S. Bien*, GLM-F110577, culture GLMC 1497.

Notes — *Pallidophorina paarla* was the most frequently isolated species from wood of *Prunus* spp. in this study; 112 isolates belonged to this species, of which seven were included

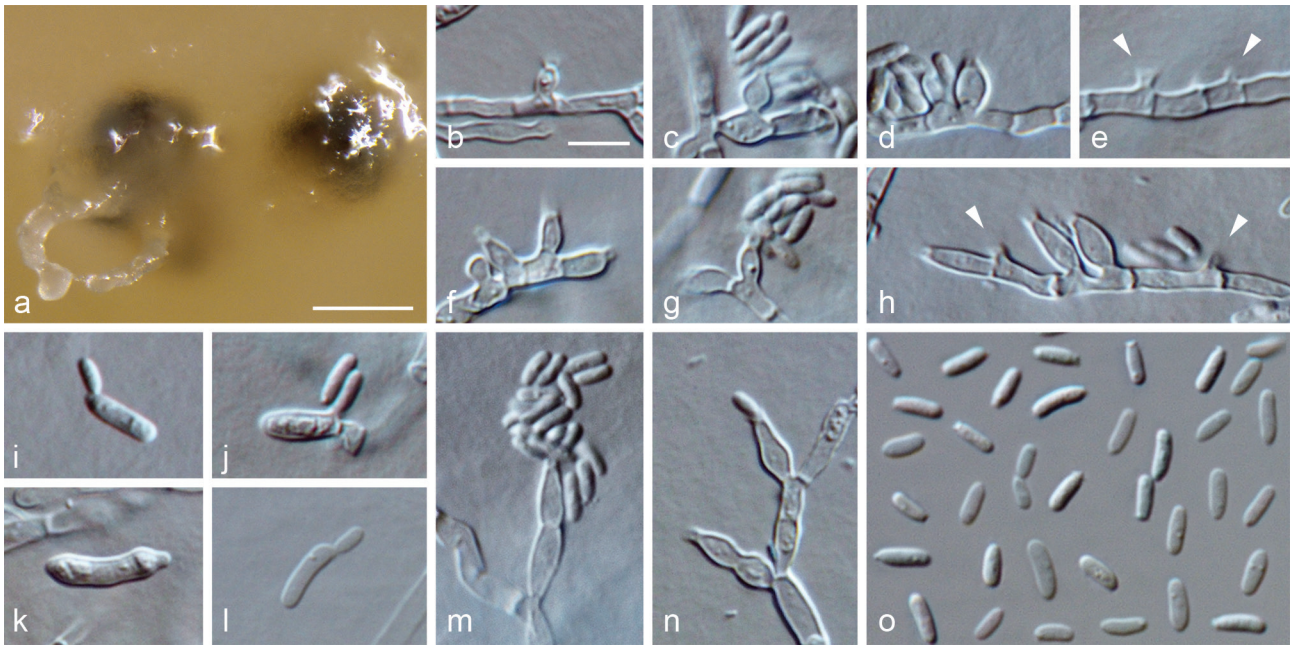

Fig. 10 *Tympanis inflata*. a. Conidiomata; b–h, m–n. conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings); i–l. mother cells (arrows indicate conidiogenous openings); o. conidia formed on hyphal cells. a. From OA; b–o. from SNA. a. SM; b–o. LM. — Scale bars: a = 200 µm, b = 5 µm; scale bar of b applies to c–o.

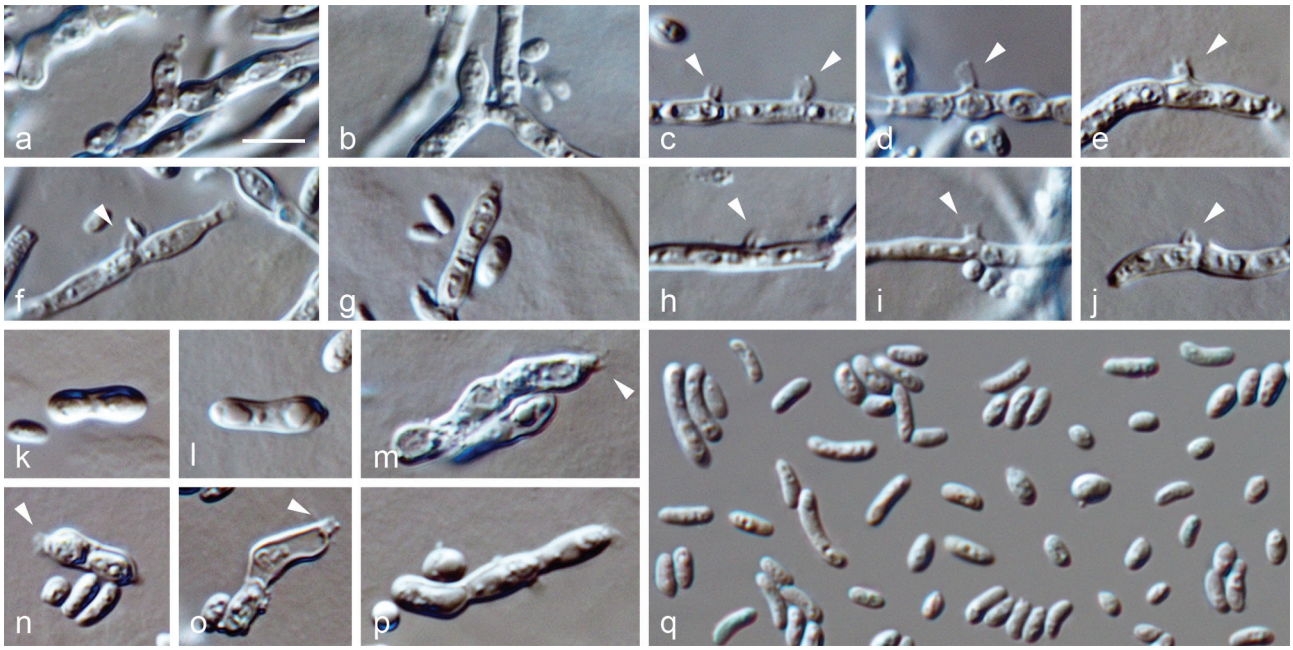

Fig. 11 *Variabilispora flava*. a–j. Conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings or short necks); k–p. mother cells (arrows indicate conidiogenous openings); q. conidia formed on hyphal cells. a–q. From SNA. a–q. LM. — Scale bar: a = 5 µm; scale bar of a applies to b–q.

in the molecular study (GAPDH sequences of strains isolated in this study are not available). It was isolated from *P. avium*, *P. cerasus* and *P. domestica* in Saxony, Lower Saxony and Baden-Württemberg. It was not found in any spore traps in this study, however in spore traps attached to *Prunus* trees in the study of Fischer et al. (2016).

Ramoconidiophora S. Bien & Damm, *gen. nov.* — MycoBank MB829161

Etymology. Name reflects the frequently branched conidiophores in conidiomata (*ramus* Lat. = branch).

Type species. *Ramoconidiophora euphorbiae* (S. Nasr et al.) S. Bien & Damm.

Colonies slow-growing, moist, white, buff or cream, lacking aerial mycelium. *Sporulation* conidia formed in conidiomata, on hyphal cells and by microcyclic conidiation. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, intercalary, reduced to discrete phialides or more often with collarettes formed directly on hyphal cells. *Conidia* aggregated in masses around the hyphae and on the agar surface. *Conidiomata* solitary or aggregated, immersed to superficial, subglobose, unilocular, wall composed of angular to roundish cells, dehiscence irregular, appearing cup-shaped when mature. *Conidiophores* hyaline, branched, septate, constricted at the septa. *Conidiogenous cells* enteroblastic, hyaline, conidiogenous loci formed laterally in each cell just below the septum as well as terminally (acropleurogenous). *Conidia* of conidiomata and intercalary hyphal cells small, hyaline, 1-celled, cylindrical, straight or slightly curved.

Ramoconidiophora euphorbiae (S. Nasr et al.) S. Bien & Damm, *comb. nov*. — MycoBank MB829163; Fig. 3e

Basionym. *Collophorina euphorbiae* S. Nasr et al., Mycol. Progr. 17: 762. 2018.

A description is provided by Nasr et al. (2018).

Tympanis inflata S. Bien, C. Kraus & Damm, *sp. nov.* — MycoBank MB829150; Fig. 3f, 10

Etymology. Named after the inflated phialides.

Typus. Germany, Rhineland-Palatinate, west of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from a spore trap mounted on vine of *V. vinifera*, 10 Nov. 2016, *C. Kraus* (GLM-F112546 holotype; GLMC 1856 = CBS 144844 = DSM 107852 = JKI-Nov7 culture ex-type).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled, 1–2.5 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed on hyphal cells and by microcyclic conidiation. *Conidiophores on hyphae* hyaline, smooth-walled, simple or septate, sometimes branched, often reduced to conidiogenous cells, directly formed on hyphae, constricted at the septa and at the base, conidiogenous loci formed terminally and rarely intercalary, immediately below the septum, 5–30 × 2–3 µm, rarely up to 60 µm long. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, often reduced to mere openings with collarettes formed directly on hyphal cells, adelophialides or discrete phialides, mostly ampulliform, sometimes navicular, often constricted at the base, 2–9 × 2–3 µm, with short tubular to funnel-shaped collarettes, opening 1–1.5 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, oblong, often slightly curved, with obtuse ends, sometimes with a prominent scar on one end, (3–)3.5–4.5(–5) × (1–)1.5–2 µm, mean ± SD = 4 ± 0.6 × 1.5 ± 0.1 µm, L/W ratio = 2.7. *Conidiomata* on OA and SNA after > 8 wk rare, immersed to erumpent, 120–350 µm, brown to black, remaining sterile. *Endoconidia* not observed. *Microcyclic conidiation* occurs from flaring collarettes at one end of conidia that have developed into mother cells, often thick-walled, sometimes septate, > 5 µm long, 2–3 µm wide.
Colonies on OA flat to very low convex with entire margin, lacking aerial mycelium, whitish to buff, reverse same colours, 18–20 mm diam in 2 wk, 32–36 mm diam in 4 wk; *on SNA* flat with entire to dentate margin, lacking aerial mycelium, white, reverse same colour; 4–6 mm diam in 2 wk, 8–10 mm diam in 4 wk.

Notes — This species was isolated only once from a spore trap in Rhineland-Palatinate. Like other species of collophorina-like fungi described in this study, namely *Capturomyces funiculosus*, '*Collophorina*' *aceris*, *Pallidophorina paarla*, *Ramoconidiophora euphorbiae*, *Vexillomyces palatinus* and *Ve. verruculosus*, it does not produce any pigments on OA medium. Phylogenetic analyses places this species in the genus *Tympanis* with the closest relatives being *T. saligna* and *T. tsugae* with 13 and 19 nucleotide differences in the LSU and ITS, respectively. *Tympanis inflata* frequently produces small inflated phialides, which distinguishes it from any other species of collophorina-like fungi. Conidia are relatively small and narrow, similar to those of species of *Vexillomyces* described in this study, however less curved. Conidial stages of several *Tympanis* species are described as conidiomatal (Groves 1952); morphological comparison with them is hindered since observed conidiomata in *T. inflata* remained sterile. In a blastn search in GenBank, the ITS sequence of *T. flava* showed a 98 % identity (100 % coverage) with a fungus (KP990974) isolated from a healthy leave of *Juniperus deppeana* in the US (Huang et al. 2016).

Variabilispora S. Bien, C. Kraus & Damm, *gen. nov.* — MycoBank MB829155

Etymology. Named after the variable spore formes (*variabilis* Lat. = variable).

Type species. *Variabilispora flava* S. Bien, C. Kraus & Damm.

Colonies slow-growing, moist, sulphur to pure yellow colours on oatmeal agar medium, lacking aerial mycelium. *Sporulation* conidia formed on hyphal cells and by microcyclic conidiation. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, intercalary, reduced to short adelophialides and discrete phialides or more often with collarettes formed directly on hyphal cells. *Conidia* aggregated in masses around the hyphae and on the agar surface. *Conidia* of intercalary hyphal cells small, hyaline, 1-celled, subglobose, ellipsoidal, oblong to allantoid, often slightly curved.

Variabilispora flava S. Bien, C. Kraus & Damm, *sp. nov.* — MycoBank MB829156; Fig. 3g, 11

Etymology. Named after its yellow (Lat.: *flavus*) colonies on OA.

Typus. Germany, Rhineland-Palatinate, west of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from a spore trap mounted on vine of *V. vinifera*, 23 Nov. 2016, C. *Kraus* (GLM-F112547 holotype; GLMC 1858 = CBS 144845 = DSM 107777 = JKI-Nov103 culture ex-type).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled, 1–3.5 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed on hyphal cells and by microcyclic conidiation. *Conidiophores on hyphae* hyaline, smooth-walled, simple or septate, constricted at the septa and at the base, mostly reduced to conidiogenous cells, directly formed on hyphae, conidiogenous loci formed terminally and sometimes intercalary, immediately below the

septum, 5–10 × 1.5–2 µm. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled, mostly reduced to mere openings with collarettes or short necks formed directly on hyphal cells, discrete phialides and adelophialides rare, hyaline, smooth-walled, ampulliform, navicular to subulate, often constricted at the base, 2–9 × 1.5–2.5 µm; short cylindrical necks rare, 1–2 × 1–2.5 µm; collarettes tubular or funnel-shaped, < 1–1.5 µm long, opening < 1–2 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, subglobose, ellipsoidal, oblong to allantoid, often slightly curved, with both ends rounded, (2–)2.5–6.5(–9) × (1–)1.5–2(–2.5) µm, mean ± SD = 4.5 ± 1.8 × 1.8 ± 0.3 µm, L/W ratio = 2.5. *Conidiomata* and *endoconidia* not observed. *Microcyclic conidiation* occurs from flaring or hardly visible collarettes at one or sometimes both ends of conidia that have developed into mother cells, often thick-walled, sometimes septate, > 5 µm long, 2.5–3.5 µm wide.
Colonies on OA flat to very low convex with dentate to fimbriate margin, lacking aerial mycelium; sulphur yellow to pure yellow; reverse same colours, 6–10 mm diam in 2 wk, 12–16 mm diam in 4 wk; *on SNA* flat with fimbriate to rhizoid margin, lacking aerial mycelium, whitish; reverse same colour; 2–4 mm diam in 2 wk, 4–6 mm diam in 4 wk.

Notes — One isolate of *V. flava* has been isolated from a spore trap in Rhineland-Palatinate. It differs from any other species of collophorina-like fungi by its sulphur yellow to pure yellow colour on OA and conidia that are very variable in shape, from almost globose, elongated to allantoid. The closest relatives of *V. flava* are *Aotearoamyces nothofagi*, '*Collophorina*' *aceris* and *Pallidophorina paarla*. In contrast to *A. nothofagi* that produces vermiform conidia on well-developed conidiophores arranged in small synnematous structures (Quijada et al. 2018), *V. flava* produces subglobose, ellipsoidal, oblong to allantoid conidia directly on hyphal cells, on reduced conidiophores or by microcyclic conidiation. Both species differ in 15, 21, 69 and 29 nucleotide differences in the LSU, ITS, *EF-1α* and *GAPDH* sequences, respectively. *Variabilispora flava* differs from '*Collophorina*' *aceris*, by a lack of dark sclerotia on OA. Only the ITS sequence of '*C.*' *aceris* is available, which differs in 36 nucleotides from *V. flava*. In contrast to *Pa. paarla* the conidia of *V. flava* are very variable in shape and neither endoconidia nor conidiomata were observed. *Variabilispora flava* differs from *Pa. paarla* in 11 and 25 nucleotides in the LSU and ITS sequences, respectively. In a blastn search in GenBank, the ITS sequence of *V. flava* showed a 100 % identity (92 % coverage) with an uncultured fungus (HE998707) found in a dead branch of *Fagus sylvatica* in Greifswald, Germany (Unterseher et al. 2013).

Vexillomyces S. Bien, C. Kraus & Damm, *gen. nov.* — MycoBank MB829157

Etymology. Name refers to the pronounced flag-like collarettes (Lat.: *vexillum* = flag).

Type species. *Vexillomyces verruculosus* S. Bien, C. Kraus & Damm.

Colonies slow-growing, moist, white or buff colours on oatmeal agar medium, lacking aerial mycelium. *Sporulation* conidia formed on hyphal cells, by microcyclic conidiation or endoconidiation. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* enteroblastic, intercalary, reduced to short adelophialides, discrete phialides or more often with collarettes formed directly on hyphal cells, collarettes mostly flaring or short tubular. *Conidia* aggregated in masses around the hyphae and on the agar surface, small, hyaline, 1-celled, cylindrical to ellipsoidal. *Vegetative hyphae* and *phialides* smooth-walled or verruculose.

Vexillomyces palatinus S. Bien, C. Kraus & Damm, *sp. nov.* — MycoBank MB829158; Fig. 3h, 12

Etymology. Named after the geographical region in Germany, in which the species was isolated.

Typus. Germany, Rhineland-Palatinate, west of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from spore a trap mounted on vine of *V. vinifera*, 31 Mar. 2016, *C. Kraus* (GLM-F112541 holotype; GLMC 1852 = CBS 144842 = DSM 107851 = JKI-Mz74 culture ex-type).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled to verruculose, 1–3.5 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed on hyphal cells and by microcyclic conidiation. *Conidiophores on hyphae* hyaline, smooth-walled to verruculose, simple or septate, rarely branched, constricted at the septa

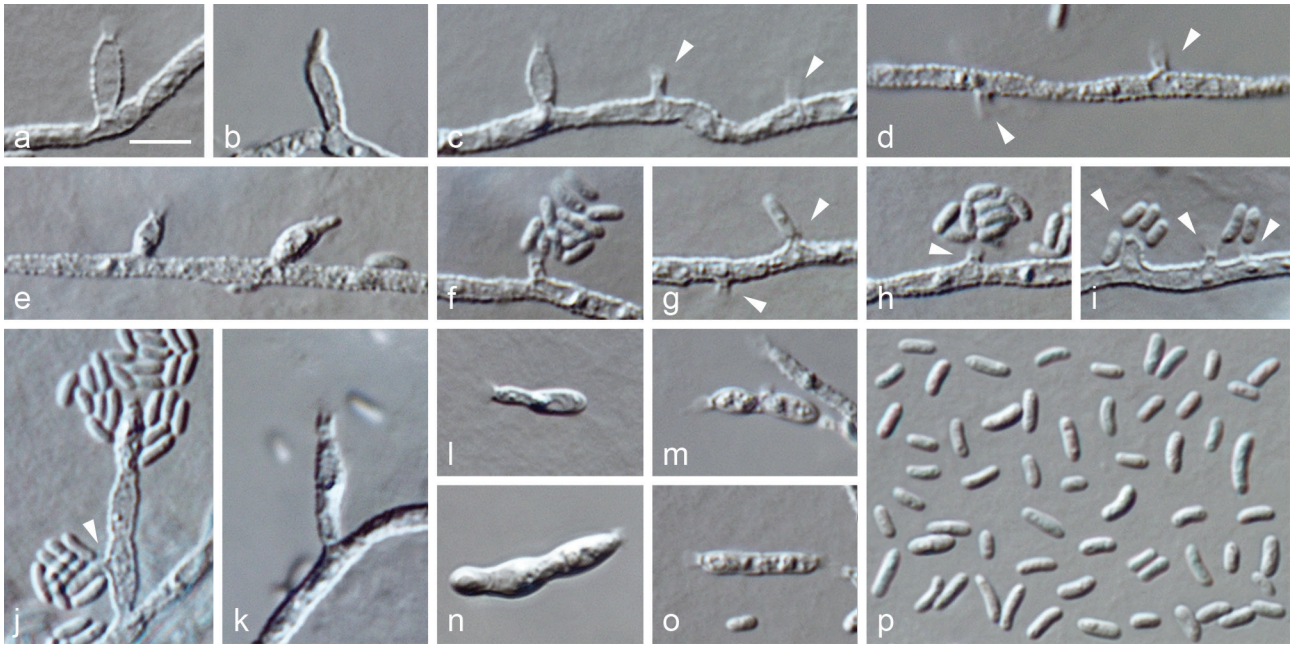

Fig. 12 *Vexillomyces palatinus*. a–k. Conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings or short necks); l–o. mother cells; p. conidia formed on hyphal cells. a–p. From SNA. a–p. LM. — Scale bar: a = 5 µm; scale bar of a applies to b–p.

and at the base, conidiogenous loci formed terminally and sometimes intercalary, immediately below the septum, mostly reduced to conidiogenous cells, directly formed on hyphae, 3–25 × 1.5–2 µm. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled to verruculose, often reduced to mere openings with collarettes or short necks formed directly on hyphal cells, discrete phialides or adelophialides, navicular to subulate, often constricted at the base, 3–13 × 1.5–3 µm, short necks cylindrical, 0.5–2 × 1–1.5 µm, collarettes mostly flaring or short and tubular, 0.5–2.5 µm long, opening 1–1.5 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, oblong, often curved, with both ends rounded, sometimes with barely visible papillate appendage on one end, (2.5–)3–4(–4.5) × 1–1.5(–2) µm, mean ± SD = 3.4 ± 0.6 × 1.3 ± 0.2 µm, L/W ratio = 2.6. *Conidiomata* and *endoconidia* not observed. *Microcyclic conidiation* occurs from flaring collarettes at one or sometimes both ends of conidia that have developed into mother cells, > 5 µm long, 2–3 µm wide, sometimes septate.
Colonies on OA flat to very low convex with entire margin, lacking aerial mycelium; whitish to buff, after > 4 wk sometimes fulvous to sepia; reverse same colours, 4–6 mm diam in 2 wk, 12–18 mm diam in 4 wk; *on SNA* flat with crenated to dentate, sometimes rhizoid margin, lacking aerial mycelium; whitish, reverse same colour; 1–3 mm diam in 2 wk, 2–3 mm diam in 4 wk.

Notes — *Vexillomyces palatinus* was only isolated once from a spore trap in Rhineland-Palatinate. The OA cultures of *Ve. palatinus* have a pigmentless, pale appearance, similar to those of *Ve. verruculosus* and the species *Capturomyces funiculosus*, '*Collophorina*' *aceris*, *Pallidophorina paarla*, *Ramoconidiophora euphorbiae* and *Tympanis inflata*. Hyphae and phialides are often verruculose; and the collarettes of phialides, intercalary hyphal openings and of conidia mother cells during microcyclic conidiation are often considerably pronounced. These features are mostly identical with its closest relative *Ve. verruculosus*, which was also isolated from spore traps. However, endoconidia have not been observed in *Ve. palatinus*; conidia of *Ve. palatinus* are on average smaller than those of *Ve. verruculosus*. Moreover, LSU, ITS, *EF-1α* and *GAPDH* sequences of the two species differ in three, 15, 16 and 12 nucleotides, respectively. In a blastn search on GenBank, the ITS sequence of *Ve. palatinus* showed 99 % identity (4 nucleotide differences, 92 % coverage, HQ611305) with an uncultured unidentified fungus from logs of *Picea abies* in Sweden (Lindner et al. 2011), as well as with an uncultured *Collophora* sp. (6 nucleotide differences, 82 % coverage, HE998707) found in a dead branch of *Fagus sylvatica* in Greifswald, Germany (Unterseher et al. 2013).

Vexillomyces verruculosus S. Bien, C. Kraus & Damm, *sp. nov.* — MycoBank MB829159; Fig. 3i, 13

Etymology. Named after the verruculose hyphae and phialides.

Typus. Germany, Rhineland-Palatinate, east of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from a spore trap mounted on vine of *V. vinifera*, 31 Mar. 2016, *C. Kraus* (GLM-F112540 holotype; GLMC 1854 = CBS 144843 = DSM 107853 = JKI-Mz75 culture ex-type).

Sexual morph not observed. *Asexual morph on SNA. Vegetative hyphae* hyaline, smooth-walled to verruculose, 0.5–3 µm wide, lacking chlamydospores. *Sporulation* abundant, conidia formed on, rarely also inside, hyphae (endoconidia) and by microcyclic conidiation. *Conidiophores on hyphae* hyaline, smooth-walled to verruculose, simple or septate, constricted at the septa and at the base, conidiogenous loci formed terminally and sometimes intercalary, immediately below the septum, mostly reduced to conidiogenous cells, directly formed on hyphae, 3–20 × 1.5–3 µm. *Conidiogenous cells* enteroblastic, hyaline, smooth-walled to verruculose, often reduced to mere openings with collarettes or short necks formed directly on hyphal cells, discrete phialides or adelophialides, navicular to subulate, often constricted at the base, 2–12 × 1.5–3 µm; necks cylindrical, 0.5–1.5 × 1–1.5 µm; collarettes mostly flaring or short tubular, 0.5–2.5 µm long, opening 1–1.5 µm, periclinal thickening sometimes visible. *Conidia* aggregated in masses around the hyphae, hyaline, smooth-walled, aseptate, often curved, oblong with both ends rounded, (2.5–)3.5–6.5(–9.5) × 1–1.5(–2) µm, mean ± SD = 5.1 ± 1.4 × 1.3 ± 0.2 µm, L/W ratio = 3.9. *Conidiomata* not observed. *Endoconidia* rarely observed, hyaline, smooth-walled, aseptate, oblong with both

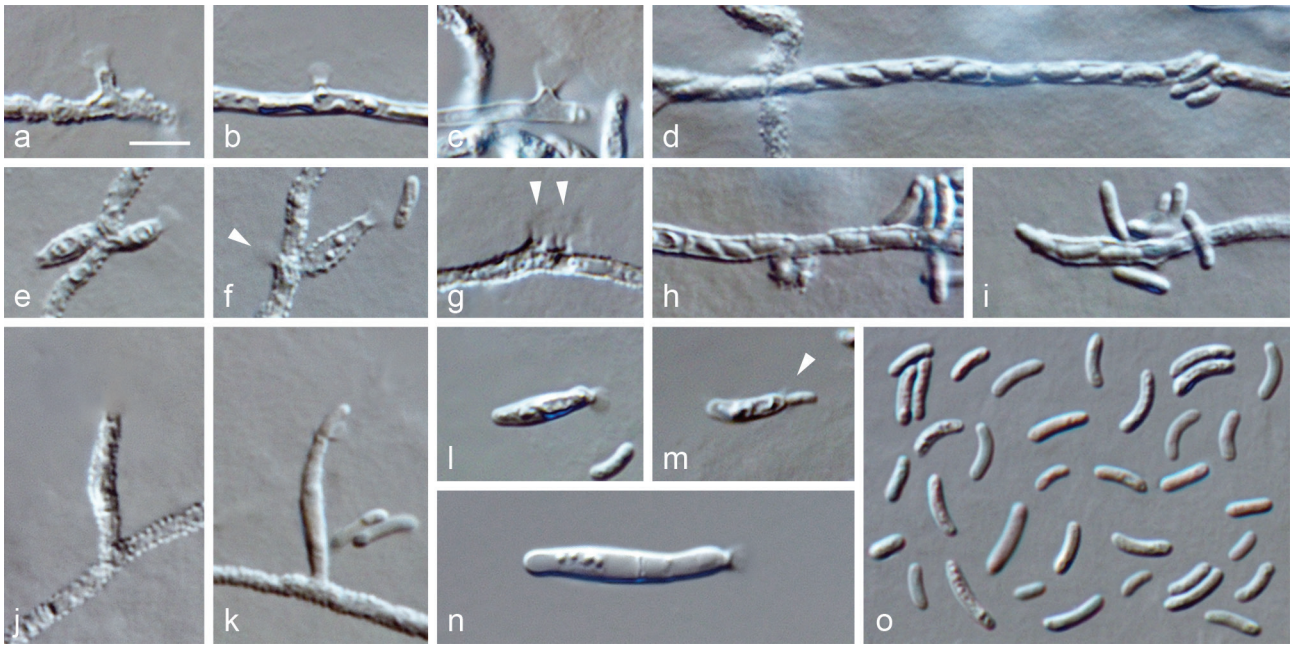

Fig. 13 *Vexillomyces verruculosus*. a–c, e–g, j–k. Conidiogenous cells formed on hyphal cells (arrows indicate conidiogenous openings); d, h–i. endoconidia; l–n. mother cells (arrow indicates conidiogenous openings); o. conidia formed on hyphal cells. a–o. From SNA. a–o. LM. — Scale bar: a = 5 µm; scale bar of a applies to b–o.

ends rounded, 2.5–3.5 × 1–1.5 µm. *Microcyclic conidiation* occurs from flaring collarettes at one or sometimes both ends of conidia that have developed into mother cells, sometimes septate, > 5 µm long, 2–3 µm wide.
Colonies on OA flat to very low convex with entire to undulate margin, lacking aerial mycelium; whitish to buff, after > 4 wk sometimes fulvous to sepia; reverse same colours, 4–6 mm diam in 2 wk, 10–14 mm diam in 4 wk; *on SNA* flat with rhizoid margin, lacking aerial mycelium; whitish, reverse same colour; < 1–2 mm diam in 2 wk, 2–8 mm diam in 4 wk.

Additional materials examined. Germany, Rhineland-Palatinate, east of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from a spore trap mounted on vine of *V. vinifera*, 23 Feb. 2017, *C. Kraus*, GLM-F112539, culture GLMC 1840 = CBS 144838 = DSM 107854 = JKI-Feb24; Rhineland-Palatinate, east of Albersweiler, research vineyard of Julius-Kühn-Institute Siebeldingen, N49°13'11.5" E8°02'34.6", from a spore trap mounted on vine of *V. vinifera*, 23 Feb. 2017, *C. Kraus*, GLM-F112538, culture GLMC 1838 = JKI-Feb21.

Notes — Three isolates of *Ve. verruculosus* were isolated from spore traps in Rhineland-Palatinate. Cultures of *Ve. verruculosus* have a pale appearance on OA medium, similar to *Ve. palatinus* and the species *Capturomyces funiculosus*, '*Collophorina*' *aceris*, *Pallidophorina paarla, Ramoconidiophora euphorbiae* and *Tympanis inflata*. Hyphae and phialides of *Ve. verruculosus* are often verruculose; and the collarettes of phialides and integrated hyphal openings as well as on conidia mother cells during microcyclic conidiation are often considerably pronounced. These features are mostly identical to its closest relative *Ve. palatinus*, which was also isolated from a spore trap. However, conidia of *Ve. verruculosus* are on average bigger than those of *Ve. palatinus.* Moreover, LSU, ITS, *EF-1α* and *GAPDH* sequences of the two species differ in three, 15, 16 and 12 nucleotides, respectively.

DISCUSSION

In all phylogenies calculated from the LSU-ITS alignment of collophorina-like species and their closest relatives, well-supported clades of formerly described *Collophorina euphorbiae* and *C. paarla* are separated from a clade containing *C. africana*, *C. hispanica* and *C. rubra* by clades of *Tympanis*, *Gelatinomyces* and a strain identified as *Claussenomyces olivaceus*. Damm et al. (2010) already discussed the formation of two clades in the original description of the genus *Collophorina* (syn. *Collophora*). Inclusion of all species into one genus was based on similar morphological features and close relatedness, as well as a lack of sequence data of further related taxa. Quijada et al. (2018), who included *C. africana*, *C. rubra* and *C. paarla* in their analyses, discussed a necessary splitting of the genus, however erroneously described the current situation of *Collophorina* as paraphyletic. Our results are in agreement with those of Quijada et al. (2018) leading to the conclusion that *Collophorina* is polyphyletic, to the separation of *C. euphorbiae* and *C. paarla* from *Collophorina*, and to the description of the new genera *Pallidophorina* and *Ramoconidiophora*. All *Collophorina* species formed a monophyletic clade and can be distinguished from *Pa. paarla*, *R. euphorbiae* and all other collophorina-like species studied here by a red pigment produced on oatmeal agar medium. Although *C. aceris* also seems to represent a different genus, we refrain from erecting a new genus in this study as neither the strain nor LSU sequence data are available.

Phylogenetic analyses recognised a high diversity of collophorina-like species in both necrotic wood of *Prunus* trees and in spore traps mounted on grapevine shoots with nine previously unknown species. Three of them are described within *Collophorina*. *Capturomyces* and *Vexillomyces* are described with two new species each, which were isolated from spore traps. One species from a spore trap did not cluster with any of the other genera, for which the new genus *Variabilispora* is described.

One isolate from a spore trap proved to belong to the genus *Tympanis* based on DNA sequence data. The genus *Tympanis* was described by Tode (1790), sanctioned by Fries (1822) and today comprises around 60 species. *Tympanis* species are inoperculate discomycetes, forming dark, gelatinised apothecia and are saprophytes or weak parasites of twigs, branches or main trunks of woody plants (Yao & Spooner 1996). In culture, *Tympanis* species form slimy, yeast-like colonies (De Hoog & McGinnis 1987) resembling cultures of *Collophorina*. The asexual morph is described as flask-shaped, erumpent and aggregated pycnidia forming dark, branched, cylindrical and filiform conidiophores. Minute conidia are produced at the apices of the conidiophores and along the sides, immediately below the septa (Groves 1952, Sutton & Funk 1975), reminiscent of those formed by *Collophorina* species. However, the isolate from this study only produced few conidiomata that remained sterile. In the past, species of *Tympanis* have been described based on the morphology of their sexual morph only. Therefore, comparison with previously described species based on morphology was not possible. Groves (1952) assessed conidial states of *Tympanis* as of no value for species identification. There is no type specimen of the type species *T. saligna* available, but Groves (1952), who revised the genus, regarded one of the two *Tympanis* species known from *Salix* at that time as *T. saligna*, which is represented by strain CBS 366.55 in our study. Most of the *Tympanis* strains included in our study originated from the study of Groves (1952) and were sequenced by Vu et al. (2019) or in this study. This is the first phylogenetic study of the genus *Tympanis*. The majority of the strains including the type species form a monophyletic clade. However, the strain '*Tympanis*' *xylophila* CBS 133220 is separated from the main clade of *Tympanis*.

A further four strains that had been identified or described as *Tympanis alnea*, *T. malicola* and *T. pseudotsugae*, including the ex-type strain of the latter (listed in Table 1) were revealed to belong to *Sordariomycetes*, *Dothideomycetes* and *Lecanoromycetes*, respectively, based on blastn searches restricted to type sequences and preliminary phylogenetic analyses (data not shown). Therefore, we excluded the respective sequences from our phylogeny. According to these results, the genus *Tympanis* is also polyphyletic. Further studies are necessary to clarify the taxonomy of these strains.

Based on the recent study on *Phacidiales* by Quijada et al. (2018), *Collophorina* s.str., *Gelatinomyces* (as *Myriodiscus*), *Pallidophorina* (as *C. paarla*), *Aotearoamyces* and *Claussenomyces prasinulus* seem to belong to the core taxa of *Tympanidaceae* (clade H in that study). The inclusion of *Holwaya*, *Mniaecia* and *Epithamnolia* in the family is questionable as the respective backbone clades were not supported. This was apparently the reason for them not to draw any taxonomic consequences from their molecular study either to confirm or to correct the previous systematics of the order (Jaklitsch et al. 2016). The same problem was encountered in our study. All taxa studied here belong to a clade sister to *Holwaya* that corresponds to clades H and K in Quijada et al. (2018). However, as we included more possible *Tympanidaceae* taxa in our phylogeny, the backbone became even more unstable, and even well-supported clades corresponding to I, J and H in Quijada et al. (2018) became blurred. As we concentrated on the collophorina-like species collected and taxa intermingling with them, we cannot make a clear circumscription of *Tympanidaceae* either.

During our survey on necrotic wood of *Prunus* spp. in Germany, collophorina-like fungi were the most abundant, with the dominating species being *Pallidophorina paarla* (syn: *C. paarla*). *Col-*

lophorina africana and *Pa. paarla* were previously reported from Germany: *C. africana* from spore traps in *Prunus armeniaca* orchards and from wood of *P. dulcis*; and *Pa. paarla* from wood of *P. persica* and *P. cerasus* and from spore traps in *Prunus* sp. (Fischer et al. 2016, Gierl & Fischer 2017). In this study, *C. africana* occurred exclusively on *P. domestica*. This is the first report of *Pa. paarla*, *C. africana* and the genus *Collophorina* in general on *P. domestica*. In contrast, *C. hispanica* that was also detected in Germany by Gierl & Fischer (2017), was not found in any of the *Prunus* orchards sampled in this study and is so far only known from *P. armeniaca* and *P. dulcis* (Gramaje et al. 2012, Arzanlou et al. 2016, Gierl & Fischer 2017).

All collophorina-like species studied here can be identified by each of the three loci, ITS, *EF-1α* and *GAPDH*. With all species, sequences of the three loci showed differences in at least four, but often more than ten nucleotides, except for the *EF-1α* sequences of *C. rubra* and *C. neorubra*, which differed in only two nucleotides.

Compared to molecular data, morphological and cultural characters were found to be less suitable for species delimitation. Single features usually apply to several collophorina-like taxa, e.g., SNA and OA cultures of all species are slow growing. However, *Collophorina* can be distinguished from all other collophorina-like genera, by the red pigmentation of OA medium (Damm et al. 2010, Gramaje et al. 2012, Xie et al. 2013, Nasr et al. 2018, this study) and forms a well-supported clade in the phylogenies. In contrast, cultures of '*C.*' *aceris*, *R. euphorbiae* (syn: *C. euphorbiae*), *Pa. paarla* (syn: *C. paarla*) and the newly described *Capturomyces funiculosus*, *Tympanis inflata*, *Vexillomyces palatinus* and *Ve. verruculosus* remain white to cream, while OA cultures of *Variabilispora flava* and *Capturomyces luteus* are yellow pigmented. The latter two species are, however, not closely related to each other.

Microscopical features are often difficult to recognise. All species of collophorina-like fungi studied here, in Damm et al. (2010), Gramaje et al. (2012) and Nasr et al. (2018) produce conidia on intercalary conidiogenous cells, on discrete phialides or adelophialides as well as by microcyclic conidiation. In most species these structures are very similar; only some of the collophorina-like species form unique features. For example, both members of the new genus *Vexillomyces*, *Ve. palatinus* and *Ve. verruculosus*, form pronounced collarettes and verruculose hyphae and phialides. *Tympanis inflata* forms short, inflated phialides, and in the microcyclic conidiation of *C. neorubra* often two or more conidia remain attached to the conidiogenous opening of the mother cells. Endoconidia have previously been found in *Ramoconidiophora euphorbiae*, *C. hispanica* and *Pallidophorina paarla*, in this study only in *Vexillomyces verruculosus*. They are therefore not regarded as a genus-specific feature. Moreover, endoconidia were only rarely observed in these four species; it is possible that other species are also able to produce endoconidia, but they were just not observed in the cultures or not formed on the substrates studied. Among the newly described species, *C. badensis*, *C. germanica*, *C. neorubra* and *Capturomyces luteus* produced fertile conidiomata. Morphology of conidiomata, conidiophores and conidiogenous cells are not distinct from those of previously described species of collophorina-like fungi, except for *Ca. luteus* in which an elongated darker area was visible in the centre of ruptured conidiomata. *Ramoconidiophora euphorbiae* differs by its conidiomatal conidiophores that predominantly develop branches at almost each septum, instead of conidiogenous openings; conidiogenous openings are almost exclusively formed terminally. *Pallidophorina* differs by its very long, tuft-like/funnel-shaped collarettes, while those of *Collophorina* and *Ramoconidiophora* are short cylindrical or even inconspicuous. There is no information on collarettes in conidiomata of *Tympanis* (Groves 1952).

Collophorina-like species were most frequently isolated from *Prunus* wood. Furthermore, they were frequently found in association with wood necroses or other wood diseases, for example on *Prunus* wood in South Africa (Damm et al. 2010), Spain (Gramaje et al. 2012), Slovakia (Ivanová & Bernadovičová 2013), Iran (Arzanlou et al. 2016) and Germany (Gierl & Fischer 2017). Additionally, *C. hispanica* was isolated on *Castanea sativa* in Spain in association with the Chestnut Red Stain disease. However, the authors argued it would be more likely that *Fistulina hepatica*, which was co-isolated with *C. hispanica*, was the causal agent of the disease (Yurkewich et al. 2017). With the exception of '*C.*' *aceris* and *R. euphorbiae*, pathogenicity was confirmed for all previously described collophorina-like species (Damm et al. 2010, Olmo et al. 2015, Arzanlou et al. 2016). In contrast, some collophorina-like species have been found in symptomless plant tissue, namely *Pallidophorina paarla* from *Prunus avium* and *P. cerasus* (Aghdam & Fotouhifar 2016), '*C.*' *aceris* from *Acer glabrum* var. *douglasii* (Xie et al. 2013) and *R. euphorbiae* from *Euphorbia polycaulis* (Nasr et al. 2018), indicating an endophytic lifestyle in at least part of their life cycle. In our survey on *Prunus* wood, most of the isolates of collophorina-like fungi originated from the transition zone of symptomatic to non-symptomatic wood tissue, while sometimes the same species was isolated from non-symptomatic wood of the same branch, which supports the assumption of a life style transition.

All species of *Collophorina* isolated from wood in this study were isolated either only from *P. avium* or only from *P. domestica*. *Pallidophorina paarla* was isolated from all hosts sampled in this study. All species, except for *C. badensis*, were isolated either only from *Prunus* wood or only from spore traps mounted on grapevine shoots. Moreover, the species from spore traps in vineyards have not previously been reported from grapevine yet, neither in Germany (Fischer et al. 2016) nor in any other country (Farr & Rossmann 2018); and no sequences of these species from grapevine tissue could be found by blastn searches on GenBank. This raises the question where these species live. Only one of the species from spore traps in vineyards, *C. badensis*, was isolated from *Prunus* wood as well, but with five nucleotides difference in *EF-1α*. However, the ITS sequences of some of these species, namely *Variabilispora flava*, *Capturomyces funiculosus*, and *Ca. luteus*, are identical with those of fungi detected in *Fagus sylvatica*, *Picea abies*, *Tsuga canadensis*, and *Pinus sylvestris* in Germany, Finland and Canada, respectively (Terhonen et al. 2011, Unterseher et al. 2013, KM Complak et al. unpubl. data, J Kaitera & HM Henttonen unpubl. data). It is therefore more likely, that all or some of these species live in adjacent fruit orchards or other trees in the neighbourhood than in grapevine.

Species of collophorina-like fungi have often been found in woody tissue. Comparatively small spores and a space-saving conidiogenesis directly on or within hyphae could be an adaption to a life inside wood and a distribution within the plant body by means of the vascular tissue system. Findings in spore traps raise the question of the distribution strategy between host plants, which becomes even more obscure as there is no proof of these species from spore traps in grapevine tissue. Usually, object slides covered with Vaseline are used as spore traps (Fischer et al. 2016, Gierl & Fischer 2017, this study). Collophorina-like species can be considered as yeast-like because of its slimy spore masses. Although distribution of fungi via air currents is well-known (Brown & Hovmøller 2002), yeast cells and spores of fungi forming moist conidia masses are more likely to be distributed by water flow, rain splash, or insects as vectors (Kluth et al. 2002, Lachance 2011). If these species live in grapevine tissue, spores are more likely to be transported from plant parts to spore traps by raindrops than by air flow. However,

if they do not live in grapevine tissue, the distribution by rain splash is unlikely as it works only over small distances. Small flies trapped in the Vaseline of the spore traps were observed during collection of the object slides (Kraus unpubl. data). This observation and a finding of *Pallidophorina paarla* in galleries of the borer *Xylotrechus arvicola* (*Coleoptera*, *Cerambycidae*) in *Prunus pisardi* (Benavides et al. 2013) support the idea of a distribution strategy via insect vectors. A report of *Collophorina* from a spore trap analysing air-borne particles of air flow (Coriolis air sampler) should be considered as doubtful as the identification of the fungus is based on an identity of the ITS2 sequence with *C. hispanica* of only 85.6 % (Fort et al. 2016). Additionally, reports of *Collophorina* from roots of *Holcus lanatus* and *Caluna vulgaris* (Kreyling et al. 2012) as well as from sedimentary rock samples from a glacier in Antarctica (Barahona et al. 2016) should also be considered doubtful, because the ITS sequence identities were < 90 %.

The high species number detected in this study and the high incidence in necrotic wood of fruit trees observed in this study and in the study of Damm et al. (2010), along with reports of collophorina-like species from four continents, demonstrate that this group of fungi is widespread, abundant and diverse. Reports of the pathogenicity of some of the species underline their potential threat at least to economically important fruit trees. Damm et al. (2010) already discussed reasons why these fungi had not been discovered for such a long time; most notably they were overlooked due to their slow growth and yeast-like appearance. Xie et al. (2013) extracted the metabolic compound Collophorin from '*C.*' *aceris*, which inhibits the growth of plant pathogens belonging to *Ascomycota*, *Basidiomycota*, *Oomycota* as well as Gram-positive and -negative bacteria. This indicates the potential importance of the compounds of these poorly studied fungi and their possible applications.

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