New species, combinations and records of *Thyronectria*, with a key to species

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Abstract

The new species *Thyronectria ulmi* is described from *Ulmus laevis* and *U. minor* collected in Austria, the Czech Republic and Slovakia. It is morphologically and phylogenetically close to the North American *T. chrysogramma*, which also occurs on *Ulmus* and shares olive green to brown muriform ascospores, but differs from the latter by geographic distribution, narrower asci, smaller ascospores with fewer septa and DNA sequence data from seven loci (ITS and LSU regions of nuclear rDNA, *ACT1*, *RPB1*, *RPB2*, *TEF1* and *TUB2* genes). As in many other *Thyronectria* species, ascomata of *T. ulmi* were closely associated with *Diplodia*, indicating a fungicolous habit. The genus *Neothyronectria* is synonymised with *Thyronectria* based on morphological and molecular phylogenetic data, and the new combinations *T. citri* and *T. sophorae* are proposed. A key to 45 accepted species of *Thyronectria* is provided. The recently described *T. abieticola*, previously known from the Czech Republic and France, is newly reported from Austria and Slovakia; its pycnidial anamorph is recorded, described and illustrated from natural substrates for the first time. A sporodochial anamorph is reported from natural substrates for *T. aurigera*, a new record for Austria as well. New host and distribution records include *T. rhodochlora* on *Acer pseudoplatanus* in Austria and *Fraxinus excelsior* in the Czech Republic, *T. sinopica* on *Hedera colchica* in the Czech Republic and *Bupleurum fruticosum* in Spain, and *T. zanthoxyli* on *Sorbus aucuparia* in Belgium and *Ulmus* sp. in the USA. *Thyronectria cucurbitula* is confirmed by sequence data from *Pinus strobus* collected in the Czech Republic, challenging the host ranges given for *T. cucurbitula* (*Pinus* subgen. *Pinus*) and *T. strobil* (*Pinus* subgen. *Strobus*), and questioning the European and Chinese records of *T. strobil*.

Keywords Ascomycota · Hypocreales · Nectriaceae · *Neothyronectria* · Phylogenetic analysis · Taxonomy

Introduction

Thyronectria Sacc. 1875 is a phylogenetically distinct genus that is morphologically well-characterised by nectriaceous ascomata covered by a yellow scurf, long, more or less persistent apical paraphyses (Jaklitsch and Voglmayr 2014) and pycnidial anamorphs in most species. Based on multi-gene phylogenies and morphology, Jaklitsch and Voglmayr (2014) and Voglmayr et al. (2016) synonymised the genera *Allantonectria*, *Mattirolia*, *Pleonectria* and *Thyronectroidea* with *Thyronectria*, and several new species were described in recent years (Jaklitsch and Voglmayr 2014; Checa et al. 2015; Voglmayr et al. 2016; Zeng and Zhuang 2017; Lechat et al. 2018; Li et al. 2018; Ma et al. 2020). Ascospores within the genus are remarkably diverse; they can be aseptate, uni-septate, transversely multiseptate or muriform with eusepta and/or distosepta, of allantoid, ellipsoid, oblong, fusiform, globose, clavate or vermiform shapes and with hyaline,

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yellowish, rosy, green or brown colouration. Ascospores of several species are budding in the ascus to produce oblong to allantoid, 1-celled, hyaline ascoconidia. A common association with effete pyrenomycetes, in particular *Diplodia* spp., indicates a fungicolous ecology of many species (Jaklitsch and Voglmayr 2014; Voglmayr et al. 2016). Currently, the genus *Thyronectria* contains 43 accepted species and for 36 of these, DNA sequence data are available.

Based on sequence data, Crous et al. (2016) established the new genus *Neothyronectria* with *N. sophorae*, a pycnidial anamorph, as generic type, which occurred on dead branches of *Sophora microphylla* collected in New Zealand. Based on a Bayesian analysis of LSU rDNA sequence data and the results of BLAST searches of ITS and LSU sequences, the genus *Neothyronectria* was considered to be closely related to but distinct from *Thyronectria*. Yang et al. (2019) added a second species from China, *N. citri*, with a teleomorph resembling *Thyronectria* in subglobose to globose ascomata with a distinct bright to greenish yellow scurf. Remarkably, the morphology of *N. citri* is notably close to the generic type of *Thyronectria*, *T. rhodochlora*, with which it shares subhyaline to hyaline muriform ascospores not budding within asci. These striking morphological similarities and the incomplete taxon and sequence sampling in the phylogenies of Crous et al. (2016) and Yang et al. (2019) call for a critical re-evaluation of the status of *Neothyronectria* as a distinct genus. Therefore, extended multigene phylogenies based on seven loci (ITS and LSU regions of nu rDNA and *ACT1*, *RPB1*, *RPB2*, *TEF1* and *TUB2* genes) were performed to evaluate whether *Neothyronectria* is congeneric with *Thyronectria*.

Recently, several fresh collections closely resembling the North American *Thyronectria chrysogramma* were made on dead branches of *Ulmus* spp. in Austria, the Czech Republic and Slovakia, but they differed by having smaller ascospores with fewer septa. Therefore, sequence data were produced to reveal whether these collections are conspecific with *T. chrysogramma* or represent a distinct undescribed species. In addition, in several fresh collections of *T. abieticola*, a pycnidial anamorph was found to be closely associated with ascomata, while in some recent collections of *T. aurigera*, a sporodochial anamorph was observed. As for these species anamorphs have not been recorded from natural substrates, pure cultures were obtained from conidia and sequenced to confirm their connection with the teleomorphs. The morphology of the ana- and teleomorphs of these collections was documented and illustrated with species descriptions provided or amended accordingly. Finally, for several *Thyronectria* species, new host associations and country records were confirmed by sequence data, which are reported here.

Materials and methods

Sample sources

Isolates investigated in this study originated from ascospores or conidia of freshly collected specimens. Details of the strains including NCBI GenBank accession numbers of gene sequences used to compute the phylogenetic trees are listed in Table 1. Strain acronyms other than those of official culture collections are used here primarily as strain identifiers throughout the work. Details of the specimens used for morphological investigations are listed in the “Taxonomy” section under the respective descriptions. Herbarium acronyms are according to Thiers (2021). Most specimens have been deposited in the Fungarium of the Department of Botany and Biodiversity Research, University of Vienna (WU-Mycologium, <https://www.jacq.org/WU-Myc#>).

Morphological observations

Microscopic preparations were mounted in water, 3% potassium hydroxide (KOH), or lactic acid (LA). Study of macromorphology was done by using a Nikon SMZ 1500 or a Nikon SMZ 18 stereomicroscope (Nelville, NY) equipped with a Nikon DS-U2 digital camera or a Keyence VHX-6000 Digital Microscope (Mechelen, Belgium). For light microscopy, a Zeiss Axio Imager.A1 compound microscope (Oberkochen, Germany), equipped with Nomarski differential interference contrast (DIC) optics and a Zeiss Axiocam 506 colour digital camera or a DIC microscope Nikon Eclipse Ni-U and a Nikon DS-Ri2 camera, was used. Photographs and measurements were taken by using the NIS-Elements D v. 3.0 or Zeiss ZEN Blue Edition software. For certain images of ascomata or conidiomata, the stacking software Zerene Stacker version 1.04 (Zerene Systems LLC, Richland, WA, USA) was used. Measurements are reported as maxima and minima in parentheses and the mean plus and minus the standard deviation of a number of measurements given in parentheses.

Culture observations

Cultures were prepared and maintained as described previously (Jaklitsch 2009) except that sometimes also 3.9% potato dextrose agar (PDA: VWR, Radnor, Pennsylvania) was used for isolation. Germinating ascospores/conidia were placed on PDA or CMD (CMA: Sigma, St Louis, Missouri; supplemented with 2% (w/v) D(+)-glucose-mono-hydrate). Cultures used for the study of anamorph micro-morphology were grown on PDA at room temperature.

Table 1 Isolates and accession numbers used in the phylogenetic analyses; those in bold were isolated/sequenced in the present study

Species	Isolate No	Herbarium No	Substrate/host	Country	GenBank accession numbers						
					ACT1	ITS	LSU	RPB1	RPB2	TEF1	TUB2
<i>Nectria asiatica</i>	MAFF 241439	BPI 879972	unid. dead bark	Japan	HM484505	HM484701	HM484563	–	JQ014140	–	HM484604
<i>N. cinnabarina</i>	CBS 125165	BPI 879981	<i>Aesculus</i> sp.	France	HM484503	HM484548	HM484562	HM484577	JQ014125	HM484527	HM484606
<i>N. dematioides</i>	CBS 126570	BPI 749337	unid. dead bark	USA	HM484502a	HM484557	HM484561	HM484576	JQ014144	HM484534	HM484603
<i>N. nigrescens</i>	CBS 125148	BPI 871083	unid. dead twigs	USA	HM484618	HM484707	HM484720	HM484781	JQ014123	HM484672	HM484806
<i>Septofusidium berolinense</i>	CBS 731.70				KM231250	KM231841	KM231722	KM232274	KM232417	KM231978	KM232112
<i>S. herbarum</i>	CBS 265.58		<i>Urtica dioica</i>	UK	KM231251	KM231842	KM231723	KM232275	KM232418	KM231979	KM232113
<i>Thyronectria abieticola</i>	CBS 128932	LJP	<i>Abies alba</i>	France	–	KX897141	–	–	–	–	–
<i>T. aquifolii</i>	THYA	WU 44628	<i>Abies grandis</i>	Austria	OL452002	OL439231	OL439231	OL440128	OL440134	OL440146	OL440154
<i>T. asturiensis</i>	CBS 125027	WU 30360	<i>Ilex aquifolium</i>	UK	KJ570663	HM534891	HM534891	KJ570715	HM534881	HM534870	KJ570638
<i>T. atrobrunnea</i>	CBS 136000	WU 32124	<i>Quercus ilex</i>	Spain	KJ570664	KJ570690	KJ570690	KJ570716	KJ570741	KJ570760	KJ570639
	CGMCC 3.11739	HMAS 271280	<i>Eleutherococcus senticosus</i>	China	–	KT423111	KT423108	KT423102	–	KX372534	KT423105
<i>T. aurigera</i>	CBS 109874	BPI 841465	<i>Fraxinus excelsior</i>	France	HM484511	HM484551	HM484573	HM484586	–	HM484521	HM484600
	THAU	WU 44631	<i>Fraxinus excelsior</i>	Austria	OL452003	OL439232	OL439232	–	OL440135	OL440147	OL440155
<i>T. austroamerica</i>	THAU1	WU 44632	<i>Fraxinus excelsior</i>	Austria	OL452004	OL439233	OL439233	OL440129	OL440136	OL440148	OL440156
<i>T. cana</i>	GG	WU 32664	<i>Gymnocladus dioica</i>	Austria	KJ570665	KJ570691	KJ570691	KJ570717	KJ570742	KJ570761	KJ570640
<i>T. balsamea</i>	CBS 125137	NCSU	<i>Abies fraseri</i>	USA	JF832454	JF832599	JF832729	JF832805	JQ014142	JF832561	JF832849
<i>T. berberidicola</i>	XJAU 1366–1	XJ-FPL 1366	<i>Berberis heteropoda</i>	China	MK838542	MK838546	MK838550	–	–	MK838554	MK838558
<i>T. berberidis</i>	CBS 144512	XJ-FPL 2177	<i>Berberis heteropoda</i>	China	MH015318	MH015314	MH015322	–	–	MH015326	MH015331
<i>T. berolinensis</i>	CBS 127382	WU 30361	<i>Ribes sanguineum</i>	Austria	KJ570666	HM534893	HM534893	KJ570718	HM534883	HM534872	KJ570641
<i>T. boothii</i>	CBS 128977	BPI 881052	<i>Picea abies</i>	Slovakia	JF832475	JF832617	JF832755	JF832796	–	JF832552	JF832871
<i>T. caraganae</i>	TCA	WU 35.938	<i>Caragana arborea</i> scens	Ukraine	KX514381	KX514384	KX514384	KX514389	–	KX514395	KX514398
<i>T. caudata</i>	CBS 136003	WU 32130	<i>Berberis cretica</i>	Greece	KJ570667	KJ570692	KJ570692	KJ570719	KJ570743	KJ570762	KJ570642
<i>T. chrysogramma</i>	CBS 141087	WU 35.942	<i>Ulmus americana</i>	Canada	KX514383	KX514386	KX514386	KX514391	KX514392	KX514397	KX514400
<i>T. citri</i>	CFCC 53590	BJFC-S1770	<i>Citrus maxima</i>	China	–	MK861080	MK861071	–	–	MK902788	MK902797
	CFCC 53591	BJFC-S1771	<i>Citrus maxima</i>	China	–	MK861081	MK861072	–	–	MK902789	MK902798
<i>T. concentrica</i>	CBS 121121	BPI 878442	<i>Agave americana</i>	Italy	HM484514	HM484547	HM484572	HM484587	KM232409	HM484524	HM484609
<i>T. coryli</i>	CBS 137264	WU 32129	<i>Corylus avellana</i>	Austria	KJ570669	KJ570693	KJ570693	KJ570721	KJ570744	KJ570763	KJ570644
<i>T. cucurbitula</i>	CBS 259.58		<i>Pinus sylvestris</i>	Netherlands	GQ505974	HM484541	GQ505998	GQ506028	JQ014131	HM484530	HM484592
	THST1	WU 44641	<i>Pinus strobus</i>	Czech Republic	–	OL439234	OL439234	–	OL440137	OL440149	OL440157

Table 1 (continued)

Species	Isolate No	Herbarium No	Substrate/host	Country	GenBank accession numbers						
					ACT1	ITS	LSU	RPB1	RPB2	TEF1	TUB2
<i>T. giennensis</i>	CBS 139474	AH 47011	<i>Quercus ilex</i> ssp. <i>rotundifolia</i>	Spain	KR057941	KR057943	KR057943	KR057945	KR057947	KR057949	KR057951
<i>T. ilicicola</i>	CBS 125147	BPI 880698	<i>Ilex aquifolium</i>	UK	HM484506	HM484538	HM484565	HM484579	–	HM484522	HM484590
<i>T. lamyi</i>	CBS 137263	WU 32159	<i>Berberis vulgaris</i>	Austria	KJ570672	KJ570695	KJ570695	KJ570723	KJ570746	KJ570765	KJ570647
<i>T. obscura</i>	CBS 136923	WU 32142	<i>Tamarix tetrandra</i>	Austria	KJ570673	KJ570699	KJ570699	KJ570724	KJ570747	KJ570766	–
<i>T. okinawensis</i>	CBS 129369, MAF 241410	BPI 881058, TUA-TPP-h92	<i>Castanopsis</i> sp.	Japan	JF832451	JF832674	JF832751	JF832827	–	JF832585	JF832878
<i>T. orientalis</i>	CGMCC 3.11741	HMAS 252896	<i>Pinus</i> sp.	China	–	KT423110	KT423107	KT423101	–	KX372535	KT423104
<i>T. pinicola</i>	CBS 125166	BPI 881059	<i>Pinus sylvestris</i>	Germany	HM484508	HM484540	HM484567	HM484580	–	HM484528	HM484591
<i>T. pistaciae</i>	CBS 139475	AH 45402	<i>Pistacia lentiscus</i>	Spain	KR057942	KR057944	KR057944	KR057946	KR057948	KR057950	KR057952
<i>T. quercicola</i>	CBS 128976	BPI 871328	<i>Quercus ilex</i> ssp. <i>rotundifolia</i>	Spain	JF832450	JF832624	JF832743	JF832831	KM232411	JF832581	JF832880
<i>T. rhodochlora</i>	CBS 136006	WU 31656	<i>Acer campestre</i>	Austria	KJ570678	KJ570704	KJ570704	KJ570729	KX514394	KJ570771	KJ570651
	NP13	WU 44642	<i>Acer pseudoplatanus</i>	Austria	–	OL439235	OL439235	OL440130	OL440138	OL440150	OL440158
<i>T. rosellinii</i>	CBS 129162	BPI 881066	<i>Abies balsamea</i>	USA	JF832474	JF832614	JF832739	JF832820	–	JF832578	JF832870
<i>T. roseovirens</i>	CBS 135999	WU 32154	<i>Laburnum alpinum</i>	Italy	KJ570683	KJ570709	KJ570709	KJ570734	KJ570754	KJ570776	KJ570656
<i>T. sinensis</i>	CGMCC 3.11740	HMAS 271282	<i>Pinus</i> sp.	China	–	KT423109	KT423106	KT423100	–	KX372533	KT423103
<i>T. sinopica</i>	CBS 127386	WU 30364	<i>Hedera helix</i>	Austria	KJ570689	HM534900	HM534900	KJ570740	HM534890	HM534879	KJ570662
	THYB	WU 44644	<i>Bupleurum fruticosum</i>	Spain	OL452005	OL439236	OL439236	OL440131	OL440139	OL440151	OL440159
<i>T. sophorae</i>	CBS 142094	CBS H-22880	<i>Sophora microphylla</i>	New Zealand	–	KY173470	KY173559	–	–	–	KY173619
<i>T. strabi</i>	CBS 125107	NY	<i>Pinus strobus</i>	USA	JF832467	JF832605	JF832725	JF832813	–	JF832569	JF832861
<i>T. ulmi</i>	TCH1 = CBS 147674	BRA CR33224, WU 44633	<i>Ulmus laevis</i>	Slovakia	OL452006	OL439237	OL439237	OL440132	OL440140	OL440152	OL440160
	TCH2	WU 44634	<i>Ulmus laevis</i>	Austria	–	OL439238	OL439238	–	OL440141	–	–
	TCH3	WU 44638	<i>Ulmus minor</i>	Czech Republic	–	OL439239	OL439239	–	OL440142	–	–
	TCH4	WU 44636	<i>Ulmus laevis</i>	Austria	–	OL439240	OL439240	–	OL440143	–	–
	TCH5	WU 44637	<i>Ulmus laevis</i>	Austria	–	OL439241	OL439241	–	OL440144	–	–
<i>T. cf. virens</i>	NP10	WU 33426	<i>Ostrya carpinifolia</i>	France	KM225678	KM225684	KM225684	KM225689	–	KM225696	KM225701
<i>T. yuccae</i>	CBS 125499		<i>Yucca elata</i>	USA	KM231247	KM231836	KM231717	KM232270	HQ97730	KM231974	KM232107
<i>T. zangii</i>	HMAS 251258	HMAS 251258	<i>Populus</i> sp.	China	JX843456	JN997424	JX843458	JX843452	–	JX843454	JN997421
<i>T. zanthoxyli</i>	CBS 126113	BPI 878445	<i>Crataegus</i> sp.	France	HM484513	HM484546	HM484571	HM484585	–	HM484523	HM484599

Table 1 (continued)

Species	Isolate No	Herbarium No	Substrate/host	Country	GenBank accession numbers						
					ACT1	ITS	LSU	RPB1	RPB2	TEF1	TUB2
<i>Tilachlidium brachiatum</i>	NP11*	WU 44640	<i>Ulmus</i> sp.	USA	–	OL439242	OL439242	–	–	–	–
	NP12	WU 44639	<i>Sorbus aucuparia</i>	Belgium	OL452007	OL439243	OL439243	OL440133	OL440145	OL440153	OL440161
	CBS 363.97		<i>Agaricus</i> sp.	France	KM231248	KM231838	KM231719	KM232271	KM232414	KM231975	KM232109

*Not included in phylogenetic analyses, as only ITS-LSU sequenced

Microscopic observations were made in tap water except where noted. The plates were sealed with parafilm and incubated at room temperature. An ex-holotype culture of *T. ulmi* was deposited at the Westerdijk Fungal Biodiversity Centre (CBS-KNAW), Utrecht, The Netherlands.

DNA extraction, PCR and sequencing

The extraction of genomic DNA, PCR and sequencing of segments of seven loci, i.e. the nuclear rDNA region encompassing the internal transcribed spacers 1 and 2, along with the 5.8S, and the D1-D2 domains of the LSU (ITS-LSU), α -actin (*ACT1*) gene, RNA polymerase II subunit 1 (*RPB1*) and subunit 2 (*RPB2*) genes, translation elongation factor 1- α (*TEF1*) gene, and β -tubulin (*TUB2*) gene, was performed as reported in Jaklitsch and Voglmayr (2014) and Voglmayr et al. (2016).

Phylogenetic analyses

Published sequences of a single accession for each *Thyronectria* species served as basis for the sequence matrix. Representative sequences were selected from Hirooka et al. (2012), with additions from Jaklitsch and Voglmayr (2011, 2014), Zeng and Zhuang (2012, 2013, 2017), Checa et al. (2015), Lombard et al. (2015), Crous et al. (2016), Voglmayr et al. (2016), Lechat et al. (2018), Li et al. (2018), Yang et al. (2019) and Ma et al. (2020). The accessions were selected according to availability of markers, and if possible, ex-type sequences were used (marked with an asterisk in Fig. 1). In addition, four *Nectria* species were included, and *Septofusidium berolinense*, *S. herbarum* and *Tilachlidium brachiatum* (*Tilachlidiaceae*) were selected as outgroups according to Lombard et al. (2015). Available sequences were downloaded from GenBank; details on the sequences used in the phylogenetic analyses are provided in Table 1.

To reveal the phylogenetic position of the newly sequenced *Thyronectria* accessions, the newly generated sequences were aligned with the GenBank sequences. All alignments were produced with the server versions of MAFFT (www.ebi.ac.uk/Tools/mafft or <http://mafft.cbrc.jp/alignment/server/>) and checked and refined using BioEdit v. 7.0.4.1 (Hall 1999). For phylogenetic analyses, the sequence matrices were combined; the resulting matrix contained 6235 alignment positions from seven loci (540 from ITS, 816 from LSU, 630 from *ACT1*, 706 from *RPB1*, 1096 from *RPB2*, 1325 from *TEF1* and 1122 from *TUB2*).

Maximum likelihood (ML) analyses were performed with RAxML (Stamatakis 2006) as implemented in raxmlGUI 2.0 (Edler et al. 2021) using the ML + rapid bootstrap setting and the GTRGAMMA substitution model with 1000 bootstrap replicates. Substitution model parameters were calculated separately for the different gene regions included in the combined analyses.

Fig. 1 Phylogram of the best maximum likelihood tree (lnL = -55,221.1187) revealed by RAxML from an analysis of the combined (ITS-LSU, *ACT1*, *RPB1*, *RPB2*, *TEF1*, *TUB2*) matrix of *Thyronectria*. ML and MP bootstrap support above 50% are given above or below the branches. Strain or herbarium numbers are given following the taxon names; strains in bold red were isolated and sequenced during the present study; holo-, neo- or epitype strains/specimens are marked by an asterisk. The tree was rooted with *Sepotofusidium berolinense*, *S. herbarum* and *Tilachlidium brachiatum* (*Tilachliaceae*) according to Lombard et al. (2015)

Maximum parsimony (MP) analyses were performed with PAUP v. 4.0a169 (Swofford 2002), using 1000 replicates of heuristic search with random addition of sequences and subsequent TBR branch swapping (MULTREES option in effect, steepest descent option not in effect). All molecular characters were unordered and given equal weight; analyses were performed with gaps treated as missing data; the COLLAPSE command was set to MAXBRLEN. Bootstrap analysis with 1000 replicates was performed in the same way, but using five rounds of random sequence addition and subsequent TBR branch swapping during each bootstrap replicate, with the COLLAPSE command set to MINBRLEN.

Results

Molecular phylogeny

Of the 6235 characters of the combined matrix, 1932 were parsimony informative (148 in ITS, 114 in LSU, 150 in *ACT1*, 300 in *RPB1*, 452 in *RPB2*, 423 in *TEF1* and 345 in *TUB2*). The phylogram of the best ML tree (lnL = -55,221.1187) obtained by RAxML is shown as Fig. 1. The MP analysis revealed a single tree of length 10, 896 (not shown) that had a similar topology as the ML tree. Except for minor differences, tree topologies agree well with those of Jaklitsch and Voglmayr (2014), Checa et al. (2015) and Voglmayr et al. (2016).

The genus *Thyronectria* is highly supported in both ML (100%) and MP (99%) analyses, but as in previous analyses (e.g. Jaklitsch and Voglmayr 2014; Checa et al. 2015; Voglmayr et al. 2016; Zeng and Zhuang 2017; Li et al. 2018; Ma et al. 2020), support of deeper backbone nodes is low or absent (Fig. 1). The ML and MP analyses reveal different phylogenetic positions of the main green-spored (*T. roseovirens*) clade, which in the MP analysis is sister group to the *T. rhodochlora*-clade (not shown). Also, the clade containing *T. sinopica* has a slightly different position in the MP analysis, where it is placed in the tree as the lineage branching off next after *T. berolinensis*. However, none of these topological differences received significant MP bootstrap support.

Taxonomy and descriptions

Thyronectria abieticola Lechat, Gardiennet & J. Fourn., Ascomycete.org 10(1): 56 (2018). Figure 2, 3.

For a detailed description of the teleomorph, see Lechat et al. (2018).

Anamorph on the natural host: Pycnidia either associated with perithecia on a common hypostroma or separate, solitary or in small groups, pyriform and dark reddish brown when turgid, collapsed and blackish when dry, 200–740 µm diam, 150–320 µm high, with a distinct apical papilla, surface smooth to slightly warted. Peridium 27–36 µm thick, of two regions: an outer region of thick-walled elongate cells orange to carmine red in water, violet in 3% KOH and an inner region of subhyaline to yellowish isodiametric cells 5–10 µm diam with walls up to 1 µm thick; the interior densely clothed with numerous fascicles of conidiophores. Conidiophores densely branched up to 3 times, 22–40 µm long, and 1.5–2.5 µm wide, hyaline, smooth. Phialides terminal, solitary, long cylindrical, slightly tapering towards tip, (6.5–)9.0–12.5(–14.5) × (1.1–)1.3–1.9(–2.6) µm (*n* = 77). Conidia oblong to ellipsoidal, (2.3–)2.7–3.3(–3.9) × (1–)1.2–1.5(–1.7) µm, l/w = (1.5–)1.9–2.5(–3.5) (*n* = 159), hyaline, 1-celled, straight to scarcely curved, eguttulate, smooth.

Cultures and anamorph in culture: see Lechat et al. (2018)

Distribution: Europe (Austria, Czech Republic, France, Slovakia).

Ecology: Only known from bark of *Abies* spp., possibly fungicolous.

Specimens examined: Austria, Oberösterreich, St. Wilibald, Großer Salletwald, on dead corticated fallen branch of *Abies grandis*, soc. *Diplodia* sp., 48° 21' 10" N, 13° 42' 50" E, alt. 440 m, 16 May 2019, H. Voglmayr (WU 44628, holomorph; culture ex anamorph THYA); St. Aegidi, W of Dornedt, 48° 26' 19" N, 13° 41' 55" E, alt. 610 m, on dead corticated branches of a felled *Abies alba* tree, soc. *Diplodia* sp., 9 May 2021, H. Voglmayr (WU 44629, teleomorph). Slovakia, Poprad, Kvetnica, on fallen dead corticated twigs of *Abies alba*, soc. *Diplodia* sp., alt. 770 m, 27 Jan. 2018, A. Polhorský (BRA CR33223, holomorph); Žilina, Istebné, on upper branches and twigs of a recently fallen *Abies alba* tree, 49° 13' 12" N, 19° 12' 10" E, alt. 663 m, 15 Feb. 2018, A. Polhorský (BRA CR33222, holomorph).

Notes: The teleomorph of our collections fully agrees with the original description, which is therefore not repeated here, but we provide illustrations of the teleomorph to complement the illustrations of Lechat et al. (2018). Based on our recent Austrian and Slovakian collections, we here add the description of the newly recorded pycnidial anamorph on the natural substrate. Upon closer examination, the anamorph was present in

Fig. 2 *Thyronectria abieticola*, teleomorph (BRA CR33223). **a–c** Stromata emerging through bark. **d** Transverse section through stroma and perithecium. **e** Ostiolar canal and paraphyses in section.

f, g Peridium wall in transverse section. **h** Apical paraphyses. **i** Asci. **j** Ascospores. (all in water except e, g in KOH). Scale bars (**a–c**) 300 μ m; (**d**) 100 μ m; (**e, f**) 20 μ m; (**g–j**) 10 μ m

three of the four collections we studied. All known collections of the species were independently made within a few years in Austria, the Czech Republic, France and Slovakia on a well-investigated host genus, *Abies*, indicating that *T. abieticola* may represent a recent introduction, the origin of which is unknown. Macro- and microphotos of the teleomorph of a Czech collection are available at [http://](http://www.mykologie.net/index.php/houby/podle-morfologie/perithecia/item/3035-thyronectria-abieticola)

www.mykologie.net/index.php/houby/podle-morfologie/perithecia/item/3035-thyronectria-abieticola (accessed 20 Aug. 2021). Like most other *Thyronectria* species, *T. abieticola* is tightly associated with *Diplodia* sp., indicating a fungicolous habit. The connection of the anamorph with the teleomorph has been proven by sequences obtained from conidial and ascospore isolates.

Thyronectria aurigera (Berk. & Ravenel) Jaklitsch & Voglmayr, Persoonia 33: 195 (2014). Figure 4, 5.

Hypostromata erumpent from bark, surrounded by bark flaps or slightly projecting above the bark, well-developed, brown in water, dark purple in 3% KOH, yellow in LA, pseudoparenchymatous of *textura angularis* of cells 4–18 µm diam with walls 1–1.5 µm thick. Ascomata superficial on the hypostroma, aggregated in groups of up to 30 in round or elongated clusters 0.5–2 mm long and 0.3–0.7 mm high, 200–350 µm diam, 200–300 µm high, subglobose to globose, cupulate or not when dry, brick red to red-brown, slightly darker in 3% KOH, more or less unchanged in LA, covered with an irregularly areolate, bright sulphur yellow scaly scurf. Peridium 35–50 µm thick, of two regions: outer region 20–35 µm thick, orange in water, turning purple in 3% KOH and bright yellow in LA, composed of a *textura globulosa-angularis* of cells 4–8 µm diam with walls 1.5 µm thick, outwardly covered by a layer of yellow amorphous crystals; inner region 10–20 µm thick, composed of a *textura prismatica* of elongate thin-walled, hyaline cells. Apical paraphyses numerous, branched, anastomosing, descending to the bases of asci, 2–3.5 µm wide. Asci clavate, (49–)53–70(–82) × (10–)11–14.5(–17) µm ($n=31$), with 8 irregularly biseriate ascospores; apex undifferentiated. Ascospores (19.5–)22.5–27.2(–29.3) × (4.8–)5.5–6.7(–7.2) µm, $l/w = (3–)3.6–4.6(–5.4)$ ($n=81$), ellipsoidal, oblong to allantoid, curved, with broadly rounded ends, (3–)6–7-septate, hyaline, at maturity becoming yellowish-brown, smooth-walled, not to slightly constricted at the septum, not budding inside or outside the asci.

Anamorph on the natural host: Conidiomata sporodochial, formed below epidermis of bark, scattered to gregarious, often tightly associated with pycnidia of *Diplodia* sp., oblong, tongue-shaped, laterally compressed, erect to prostrate, 100–450 µm high, 100–270 µm wide, dark orange to orange brown, commonly lighter coloured towards the apex, surface smooth, waxy, shiny. Stroma pseudoparenchymatous, of *textura angularis* of isodiametric cells 3–12 µm diam with walls 0.5 µm thick and containing a large orange guttule 2–4 µm diam, becoming gradually smaller towards outside, the outermost cell layer bearing the densely arranged phialides covering the entire stroma. Phialides terminal, solitary, cylindrical to irregularly ampulliform, (3.3–)4.9–7.3(–9.1) × (1.4–)1.9–2.6(–3) µm ($n=70$). Conidia oblong to ellipsoidal, (2.5–)2.8–3.5(–4.3) × (0.9–)1.1–1.3(–1.5) µm, $l/w = (2.2–)2.3–3.1(–4.3)$ ($n=44$), hyaline, 1-celled, straight, with 0–3 min guttules, smooth.

Distribution: North America and Europe (Austria, Czech Republic, Germany, France, Slovakia).

Ecology: On dead corticated branches of various *Oleaceae*; in Europe only known on *Fraxinus* spp.,

constantly associated with *Diplodia* sp. and possibly fungicolous.

Specimens examined: Austria, Niederösterreich, Ringelsdorf, riverine forest of the river March, 48° 34' 13" N, 16° 55' 25" E, alt. 150 m, on dead corticated branches of *Fraxinus pennsylvanica*, soc. *Diplodia* sp., 13 Mar. 2020, H. Voglmayr & I. Greilhuber (WU 44630, teleomorph); Niederösterreich, Bruck an der Leitha, Wolfsthal, Donauauen, 48° 08' 12" N, 17° 01' 48" E, alt. 138 m, on dead corticated branches of *Fraxinus excelsior*, 20 Feb. 2021, H. Voglmayr & I. Greilhuber (WU 43964); Oberösterreich, St. Willibald, Aichet, Au, 48° 21' 13" N, 13° 41' 02" E, alt. 400 m, on dead corticated branches of *Fraxinus excelsior*, soc. *Diplodia* sp., 14 Dec. 2019, H. Voglmayr (WU 44631, holomorph; culture ex teleomorph THAU); Wien, Donaustadt, Lobau, at the Donau-Oder Kanal near Uferhaus, 48° 10' 31" N, 16° 31' 42" E, alt. 155 m, on dead corticated branches of *Fraxinus excelsior*, soc. *Diplodia* sp., 14 Mar. 2020, H. Voglmayr & I. Greilhuber (WU 44632, holomorph; culture ex anamorph THAU1).

Notes: Until recently, this species was known only from North America; however, a French collection made in 2001 (Hirooka et al. 2012) may indicate a recent introduction of the species from North America. However, as the ascomata are rather inconspicuous, the species may have been overlooked. In the past 2 years, it has also been recorded several times from Central Europe (e.g. Czech Republic, Germany, Slovakia). The abundant availability of host substrate (corticated dead twigs of *Fraxinus*), following the rapid spread of ash dieback disease caused by *Hymenoscyphus fraxineus*, may have favoured the occurrence of *T. aurigera*. The current records are the first for Austria, and a detailed search has shown that the species is actually widespread but usually overlooked on dead corticated branches of various *Fraxinus* species, where it is constantly associated with effete conidiomata of *Diplodia* sp., indicating a fungicolous habit.

We here provide an amended description of Hirooka et al. (2012) to include additional features of the teleomorph and the characters of the sporodochial anamorph on the natural substrate. Until recently, no anamorph had been known for *T. aurigera* on natural substrates, which is likely due to the development of the small orange sporodochia beneath the host bark, becoming evident only after its removal. In addition, they were observed in only two collections (WU 44631 and WU 44632). The connection of the anamorph with the teleomorph has been proven by sequences obtained from conidial and ascospore isolates.

Thyronectria citri (C.M. Tian & Q. Yang) Voglmayr, comb. nov.

Mycobank: MB 841960.

Basionym. *Neothyronectria citri* C.M. Tian & Q. Yang, in Yang, Chen, Jiang & Tian, MycoKeys 56: 56 (2019).

Fig. 3 *Thyronectria abieticola*, anamorph (a, d–g BRA CR33223; b, c, h–p WU 44628). **a** Perithecia surrounded by pycnidia (arrows) on natural substrate (rehydrated). **b**, **c** Collapsed pycnidia (dry). **d** Pycnidium in section. **e** Pycnidial wall lined with conidiophores and phialides. **f** Conidiophores arising from pycnidial wall. **g** Peridium wall in face view. **h** Sterile hyphae. **i**, **j** Squash mount of pycnidial wall in water (**i**) and KOH (**j**). **k–o** Branched conidiophores with phialides. **p** Conidia. (all vital in water). Scale bars (**a**) 300 µm, (**b**) 400 µm, (**c**) 200 µm, (**d**) 100 µm, (**e–l**) 10 µm, (**m–p**) 5 µm

Holotype: BJFC S1770

Notes: For a detailed description of the species, see Yang et al. (2019). In our phylogenetic analyses, *Neothyronectria citri* is embedded within a highly supported subclade of *Thyronectria* that also contains the generic type, *T. rhodochlora* (Fig. 1). In addition, the teleo- and anamorphs as described and illustrated in Yang et al. (2019) fully match *Thyronectria*, in particular *T. rhodochlora* with which it shares semi-immersed to erumpent ascomata in groups with distinct bright yellow scurf and hyaline to yellowish brown muriform ascospores not budding within asci. Therefore, *N. citri* is here combined in *Thyronectria*. The phylogenetic analyses of Yang et al. (2019) include neither members of the clade containing *T. rhodochlora* nor other, basal species (*T. aurigera*, *T. chrysogramma*), which evidently is the reason why *Neothyronectria* resolved as a separate sister clade in their analyses.

Thyronectria sophorae (Crous & Thangavel) Voglmayr, comb. nov.

MycoBank: MB 841959.

Basionym. *Neothyronectria sophorae* Crous & Thangavel, in Crous et al., Persoonia 37: 329 (2016).

Holotype: CBS H-22880

Notes: For a detailed description of the species, see Crous et al. (2016). *Neothyronectria sophorae* is the generic type of *Neothyronectria*, which was established as a distinct genus based on a phylogenetic placement outside *Thyronectria*. However, the phylogenetic analyses of Crous et al. (2016) contained only four species of *Thyronectria* and were solely based on LSU rDNA data, resulting in insignificant topological support for its placement. In our extended multigene analyses, *N. sophorae* clusters with high support among other *Thyronectria* species. In addition, it is revealed to be closely related to the generic type, *T. rhodochlora* (Fig. 1). No teleomorph is known for the species, but its pycnidial anamorph fully matches the genus *Thyronectria*. Based on this sound evidence, *N. sophorae* is here transferred to *Thyronectria*.

Thyronectria ulmi Polhorský, Halasů & Voglmayr, sp. nov. Figure 6, 7.

MycoBank: MB 841958.

Etymology: named after its hosts, *Ulmus* spp.

Stromata immersed to erumpent from bark, surrounded by bark flaps or projecting above the bark; inner tissue consisting of loosely to densely interwoven, (2.2–)3.1–4.6(–6.0) µm wide ($n=40$) thin-walled hyphae, in places appearing more cellular, hyaline to subhyaline; covered by a 27–60 µm thick layer of orange-red to dark brown, thick-walled, angular, (2.8–)4–7(–10.4) µm wide cells encrusted in yellow-green amorphous scurf. Scurf consisting of yellow, minute, irregular particles and druses of crystalline appearance, not staining in Cresyl blue, without change in LA, Melzer or 60% aqueous ethanol, in KOH rapidly and entirely dissolving and releasing small amount of yellow pigment. Ascomata embedded in stromatic tissue, scattered or aggregated in groups of 2–20(–40) in rounded or elongated clusters, 0.8–2(–4) mm long, 0.6–1(–2.5) mm wide ($n=25$) and 0.8–1.2 mm high, producing dark brown to black spore masses, subglobose to ovoid, not becoming cupulate upon drying, (270–)300–480(–510) µm diam in surface view ($n=10$), 330–540 µm high in section, mostly covered by stromatic tissue, subostiole, exposed regions covered by greenish yellow scurf. Peridium orange-red, dark red, brown, 39–54(–60) µm ($n=12$) wide at the sides, consisting of a thin, up to 20 µm thick, inner layer of compressed hyaline, thin-walled cells of, (8.4–)11.8–23.6(–32.2) × (2.5–)3–4.4(–5.3) µm and a pigmented outer layer of compressed, thick-walled cells of (4.0–)5.5–12(–15.7) × (2.6–)3–4.7(–6) µm ($n=40$), orange-red in KOH, (yellowish) orange in LA; cells around the ostiole small and more isodiametric. without a distinct pH-dependent colour change in KOH and LA. Ostiolar region 50–250 µm diam in surface view, concealed by the scurf when young, later black, smooth. Ostiole periphysate, 20–50 µm wide in section. Periphyses pointed, 15–30(–52) µm long, 1.2–2.2 µm wide, embedded in gelatinous matrix, projecting into the ostiole and slightly downward. Apical paraphyses numerous, indistinct in KOH, embedded in a slime matrix when young, reaching down to the base of the asci, richly branched and anastomosing, 1.8–4.3 µm wide. Asci clavate, (120–)138–170(–175) × (18–)22–26(–30) µm ($n=25$), with variably long stipe with croziers and undifferentiated apex, containing (2–4–)8 obliquely uniseriate or biseriate ascospores. Ascospores broadly ellipsoid to cylindrical, rarely clavate, straight or curved, asymmetrical, (20–)23–29(–33.5) × (9.3–)11.5–15(–16.2) µm, $l/w = (1.4–)1.7–2.4(–3.1)$ ($n=80$), muriform, eudistoseptate, with 5–8 (rarely 9) transverse and 1–3 longitudinal, less commonly oblique septa, hyaline and often more oblong when immature, turning olive green, yellow–brown or brown at maturity, smooth, not budding in the ascus, mature spores vividly green in KOH, wine red in LA.

Fig. 4 *Thyronectria aurigera*, teleomorph (**a**, **d–q** WU 44631; **b**, **c** WU 44630). **a–c** Stromata emerging through bark; arrows denoting pycnidia of *Diplodia* sp. **d** Transverse section through stroma and perithecium in KOH. **e–h** Thin section of peridium in water (**e**),

KOH (**f**) and LA (**g**, **h**) with covering stromatal layer (**h**). **i** Section of stroma tissue in water. **j** Ascus. **k** Apical paraphyses. **l–q** Ascospores in water. Scale bars (**a–c**) 300 µm; (**d**) 50 µm; (**e–q**) 10 µm

Fig. 5 *Thyronectria aurigera*, anamorph on natural substrate (**a–h, l**) and on CMD (**i–k, m**) (**a–h, l** WU 44632; **i–k, m** WU 44631). **a, b** Sporodochia below bark; arrows denoting pycnidia of *Diplodia* sp. **c, d** Transverse section through sporodochia with superficial hymenial layer of phialides. **e–h** Squash mount of hymenium, showing phi-

alides arising from globose stroma cells. **i–k** Phialides and pegs on CMD (after 3 d). **l, m** Conidia from sporodochia (**l**) and on CMD (**m**) (all in water). Scale bars (**a, b**) 300 μ m; (**c**) 50 μ m; (**d**) 10 μ m; (**e–m**) 5 μ m

Fig. 6 *Thyronectria ulmi*, teleomorph (BRA CR33224). **a–c** Stromata emerging through bark. **d** Transverse section through stroma and perithecium. **e** Peridium and covering stromatal layer. **f–h** Mature ascospores in water (**f**), KOH (**g**) and LA (**h**). **i** Mature and submature

asci. **j** Thin section of peridium. **k** Thin section of stroma (left) and peridium (right). **l** Pseudostroma tissue with periderm fragments (all vital in water except where noted). *Scale bars* (**a**) 2 cm; (**b**) 3 mm; (**c**) 500 μ m; (**d**) 100 μ m; (**e**, **i**, **k**) 20 μ m; (**f–h**, **j**, **l**) 10 μ m

Fig. 7 *Thyronectria ulmi*, anamorph (BRA CR33224). **a** Pycnidia exuding tendrils of subhyaline conidial masses. **b** Transverse section through pycnidium. **c** Pycnidial wall. **d** Conidiophores and phialides lining the pycnidium. **e** Conidia. **f** Germinating ascospore on PDA, producing conidia. **g** Colony with scattered pycnidia at the edges

(PDA, RT, 4 w). **h** Pycnidia with conidial masses in vitro. **i** Conidia in vitro, some budding. **j–l** Intercalary phialides with conidiogenous pegs on hyphae in vitro (all vital in water). Scale bars (**a**) 200 μ m; (**b**) 100 μ m; (**c**) 20 μ m; (**d–f, i–l**) 10 μ m; (**h**) 500 μ m

Anamorph on the natural host: Pycnidia either associated with perithecia on a common stroma or separate, solitary or in small groups, ellipsoid, vertically elongated, 0.3–0.4 mm diam, distinguishable from ascomata only when wet, when producing subhyaline conidial masses. Peridium yellow-orange to red-brown, 26–53 µm wide, of thick-walled, $\pm$ isodiametric cells (2.8–)4.3–8(–11) µm diam; the interior densely lined with occasionally branching conidiophores, (9.5–)15.2–29(–36) $\times$ (1–)1.4–2(–2.4) µm. Phialides terminal, solitary, long cylindrical, slightly conical, (4.1–)7–10(–11.1) $\times$ (1.4–)1.6–2(–1.9) µm. Conidia oblong-cylindrical, (2.5–)2.8–3.8(–4.3) $\times$ 1.0–1.3(–1.4) µm, l/w = (2–)2.4–3.2(–3.6) ($n=40$), hyaline, 1-celled, straight to slightly curved, eguttulate or with minute guttules, smooth.

Cultures and anamorph in culture: On PDA colony producing conidia immediately after germination (ca. 24 h), up to 58 mm diam after 18 days at room temperature; surface cream, without aerial hyphae, soon turning yellow-orange and slimy from the centre due to conidial masses; reverse pale orange, after several weeks sometimes producing pycnidia near the edge. Conidia forming mostly on short hyphal pegs, directly on vegetative hyphae or by microcyclic conidiation. Hyphae 1.3–3 µm broad, in old colonies forming thick-walled chlamydospores, 2.8–6.3 µm broad. Pegs on hyphal cells mostly solitary, terminal or lateral, conical or cylindrical, with balls of aggregated conidia at the apex, without visible collarettes, (0.9–)1.3–3(–4.5) $\times$ (0.9–)1–1.8(–3.1) µm ($n=30$). Conidia cylindrical to ellipsoid, (3–)4.6–6.6(–7.8) $\times$ (0.9–)1.2–2(–2.6) µm, l/w = (2.6–)3–4.2(–5.1) ($n=90$), straight to curved, unicellular, hyaline, smooth, with few minute, often subterminal guttules, budding.

Distribution: Central Europe (Austria, Czech Republic, Slovakia).

Ecology: On dead corticated trunks and branches of *Ulmus* spp.; associated with effete conidiomata of *Diplodia* sp. and possibly fungicolous.

Type: Slovakia, Bratislava, Bratislava – Karlova Ves, Sihoľ, 48° 08' 58.0" N 17° 01' 20.1" E, alt. 147 m, on recently fallen *Ulmus laevis* tree, stromata on corticated branches and twigs, associated with *Diplodia* sp., 10 Jun. 2020, A. Polhorský (BRA CR33224 holotype, WU 44633 isotype, holomorph; ex-holotype culture ex teleomorph CBS 147674 = TCH1).

Other material studied (all associated with *Diplodia* sp.): Austria, Niederösterreich, Engelhartstetten, Nationalpark Donauauen, 48° 09' 40.2" N, 16° 55' 24.2" E, alt. 140 m, on fallen branch of *Ulmus laevis*, 6 Mar. 2021, H. Voglmayr & I. Greilhuber (WU 44634, teleomorph; culture TCH2); Marchegg, WWF-Auenreservat Marchauen, 48° 17' 01.5"

N, 16° 53' 50" E alt. 140 m, on corticated dead branches of a standing *Ulmus laevis* tree, 22 May 2021, H. Voglmayr & I. Greilhuber (WU 44635, teleomorph); ibid, same host, 13 Nov. 2021, Voglmayr & I. Greilhuber (WU 44947, holomorph); Ringelsdorf, riverine forest of the river March, 48° 34' 17" N, 16° 55' 17" E, alt. 150 m, on corticated dead branch of a standing *Ulmus laevis* tree, 13 Mar. 2021, H. Voglmayr & I. Greilhuber (WU 44636, teleomorph; culture TCH4); Stockerau, Stockerauer Au, riverine forest along the Göllersbach, 48° 22' 46" N, 16° 11' 37" E, alt. 170 m, on dead cut corticated branches of *Ulmus laevis*, 2 May 2021, H. Voglmayr & T. Kirisits (WU 44637, anamorph; culture TCH5). Czech Republic, Morava, Olomouc, Černovířské slatiniště forest, 49° 37' 32.5" N, 17° 15' 53.7" E, alt. 210 m, on corticated fallen branch of *Ulmus laevis*, 27 Oct. 2020, V. Halasů (unpreserved, holomorph); ibid., on the same branch, 9 Dec. 2020, V. Halasů (BRNM 828,876, holomorph); ibid., 49° 37' 02.5" N 17° 16' 15.4" E, alt. 210 m, fallen crown of a young *Ulmus minor*, on corticated branches, 9 Dec. 2020, V. Halasů (PRM 955819, holomorph). ibid., same place and piece of substrate, 25 Feb. 2021, V. Halasů (WU 44638, holomorph; ex anamorph culture TCH3). Slovakia, Bratislava, Bratislava – Karlova Ves, Sihoľ, 48° 08' 58.0" N 17° 01' 20.1" E, alt. 147 m, recently fallen *Ulmus laevis* tree, on corticated branches and twigs, 4 Mar. 2020, A. Polhorský (BRA CR33231, HR B006924, holomorph).

Notes: *Thyronectria ulmi* is the closest relative of the North American *T. chrysogramma*, which also occurs on *Ulmus* and is associated with *Diplodia* sp. Both species share olive green to brown muriform ascospores, but *T. ulmi* differs from *T. chrysogramma* by geographic distribution, narrower asci, smaller ascospores with fewer septa and DNA sequence data.

Remarkably, we observed that ascospores become distinctly wine red in lactic acid, which has so far not been reported for *Thyronectria* species. When investigating other *Thyronectria* species with green ascospores, this reaction was also observed in the closely related *T. chrysogramma* and in *T. roseovirens*, but not in *T. asturiensis*, *T. giemmensis* and *T. pistaciae*, in which ascospore colour does not change at all in lactic acid.

Thyronectria zanthoxyli (Peck) Ellis & Everh. [as '*xanthoxyli*'], N. Amer. Pyren. (Newfield): 92 (1892). Figure 8.

Specimens examined. Belgium, Prov. Antwerpen, Meerhout, 51° 8' N, 5° 5' E, on dead branch of *Sorbus aucuparia*, 12 Dec. 2019, C. van Steenwinkel (WU 44639, culture NP12). USA, Ohio, Columbus, Ohio State University, 39° 59' 58.2" N 83° 00' 56.2" W, on dead branches of *Ulmus* sp., 6 Nov. 2018, D. Grootmyers (WU 44640, teleomorph; culture NP11).

Notes: As the species is rarely illustrated, we here add illustrations of the collection from Belgium. For a detailed

Fig. 8 *Thyronectria zanthoxyli* (WU 44639). **a–e** Stromata emerging through bark; in **d**, **e** with effete conidiomata of *Diplodia* sp. (white arrows). **f** Ascus. **g–l** Ascospores. **m**, **n** conidiophores from effuse

conidiation in pure culture, showing pegs, phialides and conidia (CMD, RT, 4 d) (all vital in water). Scale bars (**a**) 1 mm; (**b**, **c**) 500 μ m; (**d**, **e**) 200 μ m; (**f–n**) 10 μ m

description of the species, see Hirooka et al. (2012; under *Pleonectria zanthoxyli*). *Thyronectria zanthoxyli* was originally described from North America, where it was primarily recorded from *Zanthoxylum americanum* (Hirooka et al. 2012), to which a North American record from *Ulmus* is here added. In Europe, *T. zanthoxyli* has been previously reported from *Crataegus* in France (Hirooka

et al. 2012), and we here add a record from *Sorbus aucuparia* collected in Belgium. According to Hirooka et al. (2012), *Thyronectria zanthoxyli* is distinguished from the closely related *T. rhodochlora* and *T. virens* by mostly immersed ascomata and by distinctly curved, and from *T. rhodochlora* also by narrower, ascospores. Our ascospore measurements ((19.4–)21.2–23.6(–24.9) $\times$ (7.1–)7.8–

8.8(–9.7) μm , $l/w = (2.3\text{--}2.5\text{--}2.9\text{--}3.1)$ ($n = 50$)) largely agree with those given in Hirooka et al. (2012). However, ascospores of our collections are not as distinctly curved as illustrated in Hirooka et al. (2012) and are therefore morphologically more similar to those illustrated for *T. virens*. Finally, the sequence data unequivocally identify our collections as *T. zanthoxyli*. This demonstrates that morphological distinction between these three closely related taxa can be difficult, and then, sequence data are required for reliable species identification.

Additional new host records

Thyronectria cucurbitula (Tode) Jaklitsch & Voglmayr, Persoonia 33: 201 (2014).

Specimen examined. Czech Republic, Morava, Olomouc, Černovířské slatiniště forest, near a small lake (former sand and gravel pit), 49° 37' 9.26" N, 17° 16' 2" E, alt. 210 m, on bark of twigs of a fallen partly decorticated crown of *Pinus strobus*, 2 May 2021, V. Halasů (WU 44641, teleomorph; culture THST1).

Notes: Hirooka et al. (2012) described *Thyronectria strobis* (as *Pleonectria strobis*) from *Pinus strobus* and distinguished it from the closely related *T. cucurbitula* primarily by sequence data and by different host ranges, with hosts from *Pinus* subgen. *Strobus* for *T. strobis* and from *Pinus* subgen. *Pinus* for *T. cucurbitula*. Both species were reported to be morphologically highly similar, with slightly shorter ascospore length ranges in *T. strobis* (22–64 μm), yet widely overlapping with those of *T. cucurbitula* (33–75 μm). Both species are therefore practically impossible to separate by teleomorph morphology alone. Differences were also reported for the anamorph in pure culture, with conidia consistently formed on ellipsoid lateral phialidic pegs in *T. cucurbitula*, while additionally also flask-shaped lateral pegs were observed in *T. strobis* (Hirooka et al. 2012). Although sequence data were generated only from North American isolates from *Pinus strobus*, specimens from *P. flexilis* and *P. monticola* were also listed as *T. strobis* by Hirooka et al. (2012).

Considering that our collection from *Pinus strobus* actually represents *T. cucurbitula*, the separation of these similar species by their host range is not any more tenable. It is therefore questionable whether *T. strobis* occurs outside North America at all, as no such records have yet been confirmed by sequence data. Collection BPI 632658 from Dabroszyn (formerly Tamsel), Poland, identified by Hirooka et al. (2012) as *T. strobis*, may therefore, like our collection, actually represent *T. cucurbitula*, and also the Chinese record from *Pinus armandii* (Zeng and Zhuang 2017) that was published without sequence data needs confirmation.

Thyronectria rhodochlora (Mont.) Seeler, J. Arnold Arbor. 21: 455 (1940).

Specimens examined. Austria, Oberösterreich, Raab, Rotes Kreuz, Rothmayrberg, 48° 22' 07" N, 13° 39' 57" E, alt. 430 m, on dead fallen corticated branch of *Acer pseudoplatanus*, 23 Aug. 2020, H. Voglmayr (WU 44642, teleomorph; culture NP13). Czech Republic, Morava, Olomouc, Černovířské slatiniště forest, 49° 37' 9.96" N, 17° 15' 51.12" E, alt. 210 m, on dead twigs in a fallen crown of *Fraxinus excelsior*, 13 Nov. 2020, V. Halasů (PRM 955820, teleomorph).

Notes: For a detailed description of the species, see Jaklitsch and Voglmayr (2014). *Thyronectria rhodochlora* is commonly found on *Acer campestre* and several other hosts, but has so far not been recorded from *Acer pseudoplatanus* and *Fraxinus excelsior*. As in all other collections of the species examined, the specimens examined here are tightly associated with an effete *Diplodia* sp., indicating a fungicolous habit.

Thyronectria sinopica (Fr.) Jaklitsch & Voglmayr, Persoonia 33: 206 (2014).

Specimen examined. Czech Republic, Moravia, Olomouc, Botanic garden of Palacký University, 49° 35' 14" N, 17° 15' 07" E, alt. 215 m, on dead twigs of *Hedera colchica*, 24 Mar. 2021, V. Halasů (WU 44643, teleomorph). Spain, Jaén, Valdepeñas de Jaén, Las chorreras, 30SVG 28,511 60,458, 37° 35' 18.28" N, 3° 48' 35.04" W, altitude 957 m, on dead branches of *Bupleurum fruticosum*, 1 Jul. 2019, S. Tello S.T.01071902 (WU 44644, teleomorph; culture THYB).

Notes: *Thyronectria sinopica* is a common species with a specific occurrence on the genus *Hedera* (*Araliaceae*), in particular *H. helix* (Hirooka et al. 2012). We here add a confirmed record from *Hedera colchica*. The current Spanish collection morphologically and with its DNA sequences fully matches this *Thyronectria* species and extends its host range to *Bupleurum* from the closely related family *Apiaceae*.

Key to species of *Thyronectria* (adapted from the key in Jaklitsch and Voglmayr 2014).

Notes: The key is primarily based on teleomorph characters. Therefore, *Thyronectria sophorae* could not be included in the key, as only the pycnidial anamorph is known. Some species (e.g. from the *Thyronectria cucurbitula* species complex) can reliably only be identified by DNA sequence data. Unless otherwise noted, ascomata occur on dead host bark.

1. Ascospores aseptate, hyaline, allantoid to short-cylindrical 2
- Ascospores septate, hyaline or distinctly coloured..... 4
2. On dead bark of *Populus*; ascospores 3.5–5.5 (–6) $\times$ 0.9–1.2(–1.4) μm *T. zangii*
- On other hosts (dead leaves of *Agave*, *Yucca*)..... 3
3. On *Agave*; ascospores (3.3–)4.3–5.5(–7.3) $\times$ (0.9–) 1.2–1.6(–2) μm *T. concentrica*
- On *Yucca*; ascospores (4.5–)5.5–7.3(–9.6) $\times$ (1.1–)1.4–1.8 (–2.3) μm *T. yuccae*

4. Ascospores at maturity distinctly green to brown, muriform, distoseptate, not budding..... 5
Ascospores hyaline to yellowish or rosy, variously euseptate 10
5. Ascospores on average distinctly longer than 22 μm 6
Ascospores on average distinctly shorter than 22 μm 8
6. On *Ulmus*; transverse septa of ascospores equal, $\pm$ regular, evenly spaced; ascospores turning wine red in lactic acid, without distinct hyaline sheath in KOH when immature 7
Not on *Ulmus*; transverse septa of ascospores unequal, with first-formed 1–3 transverse septa of ascospores distinctly more pronounced than the others; ascospores irregularly muriform-septate, not turning wine red in lactic acid, 22–28(–30) $\times$ 9–13 μm , with distinct hyaline sheath in KOH when immature..... *T. giennensis*
7. On *Ulmus americana* in North America; ascospores (24–) 29–34.5(–37) $\times$ (10–)12.5–15(–17) μm *T. chrysogramma*
On *Ulmus* spp. in Europe; ascospores (20–)23–29(–33.5) $\times$ (9.5–)11.5–15(–16) μm *T. ulmi*
8. On *Fabaceae* in Southern Europe; ascospores (13–) 15–20(–25.5) $\times$ (7.5–)9–11(–13) μm *T. roseovirens*
On other hosts..... 9
9. Ascospores mostly oblong, 14–22 $\times$ 6.5–9.5 μm , often curved, with 1 longitudinal septum, cells containing one large guttule when fresh..... *T. asturiensis*
Ascospores ellipsoid to subglobose, 17–22 $\times$ 10–13 μm , straight, with 1–3 longitudinal septa, cells finely multiguttulate when fresh..... *T. pistaciae*
10. Ascospores in nature typically not budding..... 11
Ascospores in nature budding in or outside asci..... 27
11. Ascospores 1- to multiseptate but lacking longitudinal septa..... 12
Ascospores muriform..... 18
12. Ascospores (1–)6–7-septate, smooth..... 13
Ascospores 1-septate, smooth or striate..... 14
13. Perithecia red to red-brown; ascospores ellipsoid, oblong to allantoid, with broadly rounded ends, (15–) 17–21(–25) $\times$ (4.5–)5.0–6.5(–7.3) μm ; on deciduous trees (mainly *Oleaceae*) in Europe and North America *T. aurigera*
Perithecia dark brown to black; ascospores ellipsoid to fusiform, with narrowly rounded to subacute ends; (12–) 18.5–26.4(–32.5) $\times$ (4.3–)6.2–8.5(–10) μm ; on *Berberis* in East Asia (China)..... *T. berberidis*
14. Ascospores striate, ellipsoid to fusiform, (13–)14–17 (–18.5) $\times$ (4.5–)5.3–6.7(–7.3) μm ; only known from Argentina *T. pseudomissouriensis*
Ascospores smooth..... 15
15. Perithecia greenish to brownish black; ascospores (8.5–)10–13.5 $\times$ 5–7 μm ; on *Abies* *T. abieticola*
Perithecia red to red-brown; on other hosts..... 16
16. Ascospores ellipsoid to fusiform, not constricted at the central septum, (9–)10–12(–13.5) $\times$ (3.3–)4.0–5.0(–5.7) μm ; on *Citrus*, *Gelsemium* and *Ilex*..... *T. rubicarpa*
Ascospores ellipsoid to fusiform, slightly constricted at the central septum; on *Hedera*, *Bupleurum* or *Ilex*..... 17
17. On *Ilex*; ascospores ellipsoid, (9–)11–13.5(–15.5) $\times$ (4.0–) 5.5–6.8(–7.5) μm ; conidia in culture (5.5–)6.5–9.5(–12.5) $\times$ (2.0–)2.3–3.0(–3.3) μm *T. ilicicola*
On *Hedera* or *Bupleurum*; ascospores ellipsoid to fusiform, (8–)10.5–13(–14.5) $\times$ (3.7–)5.0–6.5(–8.0) μm ; conidia in culture (5.2–)6.0–11.0(–13.5) $\times$ (1.0–)1.5–2.5(–3.0) μm *T. sinopica*
18. Perithecia typically superficial on or partly immersed in a hypostroma..... 19
Perithecia surrounded by stromatic tissue..... 23
19. Perithecia partly immersed in a well-developed hypostroma; reddish grey, yellowish brown, olive brown or dark umber brown to almost black..... 20
Perithecia superficial on a hypostroma; scarlet to red-brown..... 22
20. Perithecia typically aggregated in large groups of up to 200; ascospores with 1–3 transverse septa, subglobose to ellipsoid, straight, with broadly rounded ends, (9.7–) 10–12.5(–15) $\times$ (4.8–)6.0–7.5(–10.2) μm ; on *Fabaceae*; in nature pycnidia forming tubercular to cerebriform masses; conidia ellipsoid to oblong, (1.7–)2.3–3.0(–3.5) $\times$ (1.0–)1.3–2.0(–2.5) μm *T. austroamericana*
Perithecia aggregated in groups up to 40; ascospores with (3–)4–10 transverse septa, ellipsoid to oblong-fusiform, commonly curved, with narrowly rounded ends; pycnidia in nature unknown..... 21
21. Ascospores ellipsoid to subfusiform, with (3–)4–6 transverse septa, (10–)11–20(–21) $\times$ 5–7 μm ; only known from China..... *T. orientalis*
Ascospores ellipsoid to oblong-fusiform, with (5–)7(–10) transverse septa, (14.3–)18–24(–28.4) $\times$ (4.8–)6.3–7.7(–9.2) μm ; on *Caragana* in Europe..... *T. caraganae*
22. Ascospores of two sizes: micro-ascospores allantoid to short-cylindrical, (21–)25–30(–32.5) $\times$ (8.2–)9.5–12 (–13) μm , macro-ascospores cylindrical, (37–)39–47(–49.5) $\times$ (10–)10.5–12(–13) μm ; on *Carya* in North America *T. missouriensis*
Ascospores uniform, oblong to ellipsoid, 17–25 $\times$ 6.5–8.5 μm ; on *Ribes* *T. berolinensis*
23. Saffron to sienna stroma surrounding perithecia immersed in bark, scarcely protruding, with red–orange apex; asci long and slender; on *Lonicera involucrata* and *Symphoricarpos* in the USA..... *T. lonicerae*
Perithecia immersed in yellowish stroma erumpent from bark; ascospores yellowish to rosy at maturity; asci clavate..... 24
24. Asci four-spored, ascospores ellipsoid, (17–)18–21(–23.5) $\times$ 8–9(–10) μm , on *Citrus* in East Asia (China)..... *T. citri*

- Asci eight-spored; on other hosts in Europe and North America..... 25
25. Ascospores ellipsoid or oblong, (15–)18–25 (–37) × (7–)9–12 (–16) µm; chiefly on *Acer campestre*, but also other trees in Europe..... *T. rhodochlora*
- Ascospores oblong and often curved, averaging < 9 µm wide 26
26. Ascospores (13–)16–21 (–23) µm long; mean colony diameter 14 mm on PDA after 7 days at 25 °C; chiefly on *Rhus*, but also other trees and shrubs..... *T. virens*
- Ascospores (18–)19–24 (–26.5) µm long, distinctly curved; mean colony diameter > 67 mm on PDA after 7 days at 25 °C; chiefly on *Zanthoxylum*, but also other trees and shrubs *T. zanthoxyli*
27. Ascospores budding outside asci in perithecia..... 28
- Ascospores budding inside asci..... 29
28. Ascospores 1-septate, (8.7–)10–12.5 (–13.5) × (3.7–)4.5–6.0 (–6.8) µm; in culture conidia 1-celled, ellipsoid, fusiform or allantoid, (5–)7–10 (–11.5) × (1.8–)2.0–2.8 (–3.3) µm; on *Castanopsis* in Japan..... *T. okinawensis*
- Ascospores muriform, mostly with 7 transverse septa and 1 longitudinal septum, 17–25 × 6.5–8.5 µm; in culture conidia swollen, ellipsoid, oblong-allantoid, (0–)1 (–2)-septate, (9–)10–14 (–20) × (2.2–)3.3–4.7 (–5.5) µm; on *Ribes* *T. berolinensis*
29. Ascospores 1-septate..... 30
- Ascospores multiseptate or muriform..... 32
30. Perithecia dark to blackish brown; ascospores ellipsoid to broadly fusiform, 6–10 × 2–3 µm, on *Eleutherococcus* in China..... *T. atrobrunnea*
- Perithecia red to red-brown; ascospores larger..... 31
31. Ascospores ellipsoid to fusiform, (8–)9–11 (–13) × (3.2–)4–5.5 (–6.5) µm; on *Ilex aquifolium*; in Europe *T. aquifolii*
- Ascospores cylindrical or fusiform, (8.3–)10–13 (–15) × (2.2–)2.8–4 (–5.3) µm; on *Corylus avellana* and other deciduous trees and shrubs..... *T. coryli*
32. Ascospores filiform, transversely multiseptate..... 33
- Ascospores muriform..... 37
33. Ascospores 8–15-septate, hyaline, (26–)31–44 (–49) × (1.3–)2.3–4.0 (–4.7) µm; on *Quercus ilex* ssp. *rotundifolia* *T. quercicola*
- Ascospores 8–44-septate, long-filiform, 22–75 µm long; on conifers..... 34
34. On *Abies*; ascomatal surface scaly; ascospores 8–31-septate, (22–)29–45 (–60) × (1.5–)2.0–3.2 (–4.0) µm *T. roselinii*
- On *Pinus*; ascomatal surface generally scurfy (species reliably only distinguishable by DNA sequence data)..... 35
35. Ascospores 11–27-septate, (28–)33–63 (–70) × 2.5–3.5 µm; only known from China *T. sinensis*
- Ascospores with more septa 36
36. Mostly on *Pinus* subgenus *Pinus*; ascospores 15–39-septate, (33–)43–65 (–75) × (2.3–)2.7–3.5 (–3.7) µm; confirmed by DNA data only from Europe..... *T. cucurbitula*
- On *Pinus* subgenus *Strobus*; ascospores 12–44-septate, (22–)33–52 (–64) × (2.0–)2.2–3.2 (–4.0) µm; confirmed by DNA data only from North America..... *T. strobi*
37. Ascospores disarticulating; part-ascospores subglobose to ellipsoid, (7.7–)8.7–12 (–13.5) × (5.0–)6.5–8.5 (–9.0) µm; on *Platanus occidentalis* and *Ulmus americana*; in USA *T. chlorinella*
- Ascospores not disarticulating..... 38
38. Ascospores subglobose to ellipsoid, (5.0–)5.5–7.5 (–9.5) × (4.0–)4.5–6.5 (–8.5) µm; on *Fabaceae*..... *T. sphaerospora*
- Ascospores differently shaped..... 39
39. Ascospores distinctly clavate..... 40
- Ascospores ellipsoid, oblong-clavate, cylindrical, fusoid, fusiform or vermiform 41
40. Ascospores broadly clavate with longitudinal septa not restricted to the upper (wider) part, (16–)18–23 (–36.5) × (4.3–)4.8–6.2 (–7.0) µm; ascomata collapsing; on *Ribes* in North America..... *T. clavatispora*
- Ascospores narrowly clavate with longitudinal septa only in the upper (wider) part, (21–)25–33 (–38) × (4.0–)5.0–6.2 (–7.2) µm; ascomata not collapsing; on *Berberis cretica*, *B. hispanica*, *B. cf. lycium* in Greece, Morocco, Spain and Pakistan..... *T. caudata*
41. Perithecia entirely black; ascospores fusiform, oblong, vermiform or clavate; (12.5–)17.0–24.5 (–28.5) × (3.5–)4.0–5.2 (–6.5) µm; on *Tamarix* in Europe *T. obscura*
- Perithecia at least partly with shades of red..... 42
42. Ascospores fusoid or oblong to oblong-clavate, averaging > 5 µm wide; on *Berberis*..... 43
- Ascospores ellipsoid, fusiform, cylindrical to vermiform, averaging < 5 µm wide; on conifers..... 44
43. Perithecia orange, red to red-brown, often with a darker apex; asci (94–)108–143 (–160) × (17–)18.7–26.5 (–30) µm; ascospores mostly fusoid with narrowly rounded to subacute ends, (13.5–)18.5–25.5 (–30.0) × (4.8–)5.5–7.2 (–8.2) µm *T. lamyi*
- Upper half of perithecia blackish brown, gradually turning red-brown towards the base; asci (57–)67–99 (–118) × (9–)12–21 (–26) µm; ascospores mostly oblong to oblong clavate with broadly rounded ends, (15–)19–26 (–33.5) × (3.5–)4.5–6.3 (–9) µm..... *T. berberidicola* (nom. inval.)
44. On *Picea*; perithecial wall at the apex of three regions; ascospores with 7–25 transverse septa, cylindrical to vermiform, (15.5–)20–30 (–36) × (2.8–)3.2–4.2 (–4.5) µm; in culture conidia long-cylindrical to allantoid, (7.5–)9–11 (–12.3) × (1.3–)1.5–2.0 µm..... *T. boothii*
- On *Abies* or *Pinus*; perithecial wall at the apex of two regions; ascospores averaging > 4.5 µm wide..... 45

45. On *Abies*; ascospores ellipsoid to fusiform with 5–9 transverse septa, $(16-)20-24(-28.5) \times (3-)4-5.5(-7) \mu\text{m}$; in culture conidiophores not abundant; conidia subglobose to ellipsoid, $(6.0-)6.5-7.2(-9.0) \times (2.2-)2.5-3.3(-3.5) \mu\text{m}$ *T. balsamea*
 On *Pinus*; ascospores ellipsoid, fusiform to vermiform with 5–15 transverse septa, $(14-)18-28(-46.5) \times (3.2-)4.3-5.3(-7) \mu\text{m}$; in culture conidiophores abundant; conidia oblong, slightly swollen at both ends, $(5.5-)7-11(-13) \times (1.7-)2.0-2.7(-3.0) \mu\text{m}$ *T. pinicola*

Discussion

This publication provides additional new data on the biodiversity, host range and distribution of *Thyronectria*, a nectriaceous genus. *Thyronectria ulmi* is revealed as a new species from Central Europe, being closely related to the North American *T. chrysogramma*. Both species share hosts from the genus *Ulmus* and are fungicolous on *Diplodia* sp., but differ by sequence data and morphology. Remarkably, *T. ulmi* has been collected several times mainly on dead branches of *Ulmus laevis* in riverine forests of the River Danube and the Morava/March, where it appears to be widespread. Considering that mature *Ulmus* trees have become rare in such habitats due to Dutch elm disease (previously caused by *Ophiostoma ulmi* and presently by *O. novo-ulmi*, Kirisits and Konrad 2004), it is not surprising that the fungal biodiversity on *Ulmus* hosts harbours still undescribed species. That all but one collection of *T. ulmi* were made on mature *U. laevis* likely reflects the higher abundance of this host species compared to *U. minor* in the post-epidemic period of Dutch elm disease (Kirisits and Konrad 2004). It is nevertheless possible to find *T. ulmi* on *U. minor* and younger trees as well, as shown by one of the Czech finds from ca. 20–25 years old *U. minor* (PRM 955819).

Based on the investigation of recent collections, we were also able to provide new data on asexual morphs on natural substrate for several species. Detailed morphological investigations resulted in extended species descriptions and illustrations of ana- and teleomorphs of little-known species. For the first time, we here report and describe pycnidia from natural substrate for the recently described *T. abieticola*, for which pycnidia were so far only known from pure culture (Lechat et al. 2018). In addition, for *T. abieticola*, only an ITS sequence from the type culture was available, resulting in an uncertain phylogenetic placement. We here add additional markers for this species, and in our multigene phylogeny, it is revealed as the most basal taxon of the main conifericolous clade with high (92% MP) to maximum (100% ML) bootstrap support (Fig. 1).

We here also report a new sporodochial anamorph on natural substrate for *T. aurigera*. This is remarkable, as *Thyronectria* (syn. *Pleonectria*) species usually have pycnidial anamorphs (Hirooka et al. 2012). However, also *T. concentrica*, previously known as *Allantonectria miltina*, has a sporodochial anamorph (Voglmayr et al. 2016). As *T. aurigera* and *T. concentrica* are located at basal positions in the phylogenetic analyses (Fig. 1), sporodochial anamorphs may be considered ancestral for the genus, and it is an additional argument for the inclusion of the genus *Allantonectria* in *Thyronectria* as advocated by Voglmayr et al. (2016). However, by reporting effuse sporulation on natural substrates for *T. roseovirens*, Jaklitsch and Voglmayr (2014) already pointed out that pycnidial anamorphs are not diagnostic for the genus *Thyronectria*.

Our multigene phylogenies also resolved the position of the genus *Neothyronectria* recently described by Crous et al. (2016). The results show that the genus *Neothyronectria* is not only embedded within *Thyronectria* but also closely related to the type of the genus, *T. rhodochlora* (Fig. 1). A close relationship is also supported by the teleomorph morphology of *N. citri* (Yang et al. 2019), which fully agrees with the *T. rhodochlora* group in ascomatal and ascospore characters. This corroborates that *Neothyronectria* is synonymous with *Thyronectria*, into which its two species are therefore newly combined here.

We also provide new country and host reports for other *Thyronectria* species confirmed by sequence data. *Thyronectria abieticola*, a recently described species from France (Lechat et al. 2018) is newly reported for Austria and Slovakia. Likewise, until recently, in Europe, *T. aurigera*, a primarily North American species, has been only known from France (Hirooka et al. 2012), and the current records from *Fraxinus* spp. are new for Austria. Concluded from several recent reports from Central Europe (e.g. Czech Republic, Germany, Slovakia), this species may have recently been favoured in the course of ash dieback disease, which has substantially increased the availability of suitable host substrates.

Additional new host and distribution records confirmed by sequence data include *T. rhodochlora* from *Acer pseudoplatanus* in Austria and *Fraxinus excelsior* in the Czech Republic, *T. sinopica* from *Hedera colchica* in the Czech Republic and *Bupleurum fruticosum* in Spain, and *T. zanthoxyli* from *Sorbus aucuparia* in Belgium and *Ulmus* sp. in the USA. *Thyronectria cucurbitula* is confirmed by sequence data from *Pinus strobus* collected in the Czech Republic, suggesting that *T. cucurbitula* is not confined to pine species from subgen. *Pinus* but also occurs on subgen. *Strobus*. Confirmed records of *T. strobis* are currently only known from North America. Therefore, additional sequence data are required to reveal the species identity of the European (Hirooka et al. 2012) and Chinese (Zeng and Zhuang 2017) records of *T. strobis*.

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Data availability DNA sequences used in the present study are available in NCBI GenBank. Fungal specimens are stored in public herbaria.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

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