



# Phylogenetic and taxonomic revision of *Lopadostoma*

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## Key words

*Anthostoma*  
*Anthostomella*  
*Ascomycota*  
*Diatrypaceae*  
ITS  
LSU  
*Phaeosperma*  
pyrenomycetes  
*rpb2*  
*Xylariaceae*  
*Xylariales*

**Abstract** The genus *Lopadostoma* (*Xylariaceae*, *Xylariales*) is revised. Most species formerly assigned to *Lopadostoma* do not belong to the genus. Twelve species are herein recognised, of which two are only known from morphology. Ten species, of which six (*L. americanum*, *L. fagi*, *L. insulare*, *L. lechatii*, *L. meridionale* and *L. quercicola*) are newly described, are characterised by both morphology and DNA phylogeny using LSU, ITS and *rpb2* sequences. Morphologically, ecologically and phylogenetically *Lopadostoma* is a well-defined genus comprising exclusively species with pustular pseudostroma development in bark of angiospermous trees. *Phaeosperma ailanthis*, *Phaeosperma dryophilum* and *Sphaeria linosperma* are combined in *Lopadostoma*. *Lopadostoma gastrinum* is neotypified and *L. turgidum* is lecto- and epitypified. Species with asci and ascospores similar to those of *Lopadostoma* but having perithecia immersed in wood, particularly those of *Lopadostoma* subg. *Anthostomopsis* have been determined to be unrelated to the genus. DNA data confirm that *Anthostoma* is unrelated to *Lopadostoma*. Its type and currently only confirmed species *Anthostoma decipiens* belongs to *Diatrypaceae*. DNA data also show that *L. pouzarii* and *Barrmaelia macrospora* are unrelated to *Lopadostoma*. A commentary is provided for names in *Lopadostoma* and those names in *Anthostoma* that may be putative species of *Lopadostoma* based on their protologues. *Anthostoma insidiosum* is an older name for *Anthostomella* (*Diatrype*) *adusta*.

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## INTRODUCTION

Nitschke (1867) erected the pyrenomycete genus *Anthostoma* based on *A. decipiens* (DC.) Nitschke, basionym *Sphaeria decipiens* DC. In the same work he also recognised *Anthostoma* subg. *Lopadostoma* Nitschke, which later Traverso (1906) elevated to generic rank. Nitschke had only included *Lopadostoma turgidum* in his subgenus. This species is therefore the type of the genus, contrary to Clements & Shear (1931) and von Arx & Müller (1954), who listed *L. gastrinum* as the type species of *Lopadostoma*. Læssøe (1994) accepted *Lopadostoma* in the *Xylariaceae*, as had been already concluded by Haynes (1969), based on a developmental study on '*L. gastrinum*' from *Quercus*. Martin (1969) keyed out 16 species of *Lopadostoma*, combined 13 of them invalidly, either by neglecting an earlier combination (*L. juglandinum*), by omitting the basionym or stating it as a synonym, but later he (Martin 1976) provided the basionym for 11 species and a validating diagnosis including type information for *L. stictoides*. Rappaz (1992, 1993) studied the sexual and asexual morphs of *Anthostoma decipiens* and concluded that the fungus belongs to the *Diatrypaceae* as a distinct genus close to *Eutypella*. Lu & Hyde (2000) accepted Rappaz' view. Earlier Læssøe & Spooner (1994) had combined *A. decipiens* in *Cryptosphaeria* Ces. & De Not.

Rappaz (1995) listed only *L. turgidum* and *L. gastrinum* in his *Lopadostoma* subg. *Lopadostoma*, widened the concept of the genus and erected *Lopadostoma* subg. *Anthostomopsis* for species with similar asci and ascospores but differing in perithecia that are immersed in eutypoid configuration in wood. In addition, he established *Barrmaelia* for species similar to this

subgenus, but with inamyloid ascus apices and ascospores that tend to be allantoid, i.e. being closer to the *Diatrypaceae*. Læssøe & Spooner (1994), Rappaz (1995) and Lu & Hyde (2000) provided keys to genera including *Anthostoma*, *Anthostomella* and *Lopadostoma* and others that are similar to them. The genus *Anthostomella* differs from *Lopadostoma* in that the perithecia are solitary, scattered or variously aggregated, that stromatic tissues are confined to a clypeus and that the mostly ellipsoid ascospores often have a dwarf cell, i.e. a small hyaline cellular appendage at one end. Furthermore, species of *Anthostomella* only rarely occur in branches of trees. *Lopadostoma* in a strict sense occurs always in bark of trees or shrubs with perithecia immersed in pustulate pseudostromata, referred to as stromata below; its ascospores are more or less oblong, small, never with a dwarf cell. Within so-called 'stromatic' genera closest to *Lopadostoma* are *Helicogermslita* and *Leptomassaria*, which differ by spiralling ascospore germ slits, *Helicogermslita* also by the absence of an apical apparatus. *Barrmaelia* differs mostly by inamyloid ascus apices, effused stromata and pale brown ascospores tending to be allantoid. Below we revise several species, establish new ones and also show that *Lopadostoma* subg. *Anthostomopsis* is generically different from *Lopadostoma* s.str.

## MATERIALS AND METHODS

### *Isolates and specimens*

All isolates used in this study originated from ascospores of fresh specimens. Numbers of strains including NCBI GenBank accession numbers of gene sequences used to compute the phylogenetic trees are listed in Table 1. The following strain acronyms other than those of official culture collections (Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CBS) are used here for both specimens and strains, but primarily as strain identifier throughout the work: LF, LG, LGC, LPL, LQM, LT. Representative isolates have been deposited at the

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CBS. Details of the specimens used for morphological investigations are listed in the Taxonomy section under the respective descriptions. The herbarium acronyms B, BR, CO, F, K, L, LUX, M, MPU, PAD, PC, S, TUB, UPS, WU are according to Thiers (2013). Freshly collected specimens have been deposited in the Herbarium of the Institute of Botany, University of Vienna (WU). Specimens with the acronyms CLL (Christian Lechat), JF (Jacques Fournier) and PL (Paul Leroy) are preserved in the personal herbarium of the respective collector, where no WU number is given.

### Culture preparation, growth rate determination and analysis of phenotype

Cultures were prepared and maintained as described previously (Jaklitsch 2009) except that 2 % malt extract agar (MEA; 2 % w/v malt extract, 2 % w/v agar-agar; Merck, Darmstadt,

Germany) was used as the isolation medium. Cultures used for the determination of growth rates and study of asexual morph micro-morphology were grown on 2 % MEA or potato dextrose agar (PDA, 39 g/l; Merck, Darmstadt, Germany) at room temperature, defined here as  $22 \pm 3$  °C, or at 25 °C under alternating 12 h cool daylight and 12 h darkness. Microscopic observations were generally made in 3 % KOH, rarely in water or lactic acid where noted, and amyloidity was checked with Lugol solution. Morphological analyses of microscopic characters were carried out as described earlier (Jaklitsch 2009). Data were gathered using a Nikon Coolpix 995 or Coolpix 4500 or a Nikon DS-U2 digital camera and measured by using NIS-Elements D v. 3.0 software. Methods of microscopy included stereomicroscopy using an Olympus SZ 60 or Nikon SMZ 1500 and Nomarski differential interference contrast (DIC) using the compound microscope Nikon Eclipse E600. Kornerup & Wanschler (1981) was used as the colour standard.

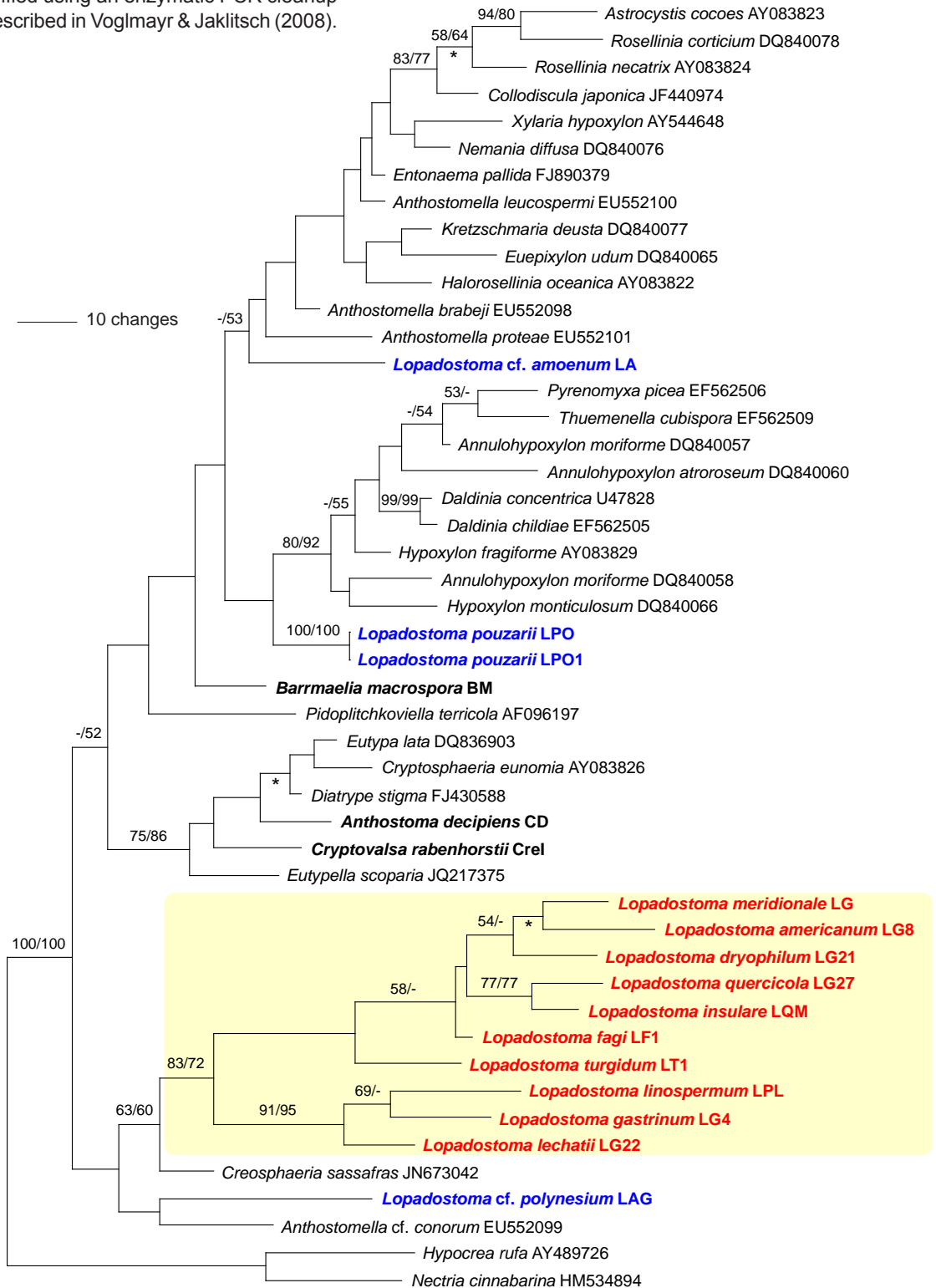
**Table 1** Strains and NCBI GenBank accessions used in the phylogenetic analyses. The asterisk (\*) denotes ex-holo-, neo- or epitype strains.

Taxon	strain*	host	GenBank accessions	
			ITS-LSU	rpb2
<i>Anthostoma decipiens</i>	CD	<i>Carpinus betulus</i>	KC774565	n.d.
<i>Barrmaelia macrospora</i>	BM	<i>Populus cf. nigra</i>	KC774566	n.d.
<i>Cryptovalsa rabenhorstii</i>	Crel	<i>Hippocrepis emerus</i>	KC774567	n.d.
<i>Lopadostoma americanum</i>	CBS 133211 = LG8*	<i>Quercus</i> sp. (white oak)	KC774568	KC774525
<i>Lopadostoma cf. amoenum</i>	MUCL 51842 = LA	<i>Fagus sylvatica</i>	KC774569	n.d.
<i>Lopadostoma dryophilum</i>	CBS 133213 = LG21*	<i>Quercus petraea</i>	KC774570	KC774526
	LG23	<i>Quercus petraea</i>	KC774571	KC774527
	LG24	<i>Quercus petraea</i>	KC774572	KC774528
	CBS 107.39 = LG41	n. a.	KC774573	KC774529
<i>Lopadostoma fagi</i>	LF	<i>Fagus sylvatica</i>	KC774574	KC774530
	CBS 133206 = LF1*	<i>Fagus sylvatica</i>	KC774575	KC774531
	LF2	<i>Fagus sylvatica</i>	KC774576	KC774532
	LF3	<i>Fagus sylvatica</i>	KC774577	KC774533
	LGC	<i>Corylus avellana</i>	KC774578	KC774534
<i>Lopadostoma gastrinum</i>	LG1	<i>Carpinus betulus</i>	KC774579	KC774535
	LG18	<i>Prunus padus</i>	KC774580	n.d.
	CBS 133210 = LG2	<i>Ulmus glabra</i>	KC774581	KC774536
	LG20	<i>Carpinus betulus</i>	KC774582	n.d.
	LG26	<i>Ulmus minor</i>	KC774583	n.d.
	CBS 134632 = LG4*	<i>Ulmus minor</i>	KC774584	KC774537
	LG5	<i>Ulmus minor</i>	KC774585	KC774538
	LG6	<i>Acer campestre</i>	KC774586	KC774539
	LG7	<i>Acer campestre</i>	KC774587	KC774540
<i>Lopadostoma insulare</i>	LG32	<i>Quercus coccifera</i>	KC774588	KC774541
	CBS 133214 = LQM*	<i>Quercus ilex</i>	KC774589	KC774542
<i>Lopadostoma lechatii</i>	CBS 133694 = LG22*	<i>Carpinus betulus</i>	KC774590	KC774543
<i>Lopadostoma linospermum</i>	CBS 133208 = LPL*	<i>Pistacia lentiscus</i>	KC774591	KC774544
	LPL1	<i>Pistacia lentiscus</i>	KC774592	KC774545
<i>Lopadostoma meridionale</i>	CBS 133209 = LG*	<i>Quercus ilex</i>	KC774593	KC774546
	LG29	<i>Quercus ilex</i>	KC774594	KC774547
	LG33	<i>Quercus coccifera</i>	KC774595	KC774548
	LG34	<i>Quercus coccifera</i>	KC774596	KC774549
	LG35	<i>Quercus ilex</i>	KC774597	KC774550
	LG36	<i>Quercus ilex</i>	KC774598	KC774551
	LG40	<i>Quercus ilex</i>	KC774599	KC774552
<i>Lopadostoma cf. polynesium</i>	LAG	<i>Amelanchier ovalis</i>	KC774600	KC774553
<i>Lopadostoma pouzarii</i>	CBS 103.96 = LPO	<i>Fraxinus excelsior</i>	KC774601	KC774554
	MUCL 47149 = LPO1	<i>Fraxinus excelsior</i>	KC774602	n.d.
<i>Lopadostoma quercicola</i>	CBS 133212 = LG12	<i>Quercus cerris</i>	KC774603	KC774555
	LG14	<i>Quercus petraea</i>	KC774604	n.d.
	LG15	<i>Quercus cerris</i>	KC774605	n.d.
	LG16	<i>Quercus cerris</i>	KC774606	KC774556
	LG17	<i>Quercus petraea?</i>	KC774607	n.d.
	LG19	<i>Quercus petraea</i>	KC774608	KC774557
	LG25	<i>Quercus</i> sp.	KC774609	n.d.
	CBS 134633 = LG27*	<i>Quercus pubescens</i>	KC774610	KC774558
	LG3	<i>Quercus suber</i>	KC774611	KC774559
	LG37	<i>Quercus cerris</i>	KC774612	n.d.
	LG38	<i>Quercus pubescens</i>	KC774613	KC774560
	LG39	<i>Quercus cerris</i>	KC774614	n.d.
	LG9	<i>Quercus cerris</i>	KC774615	n.d.
<i>Lopadostoma turgidum</i>	LT	<i>Fagus sylvatica</i>	KC774616	KC774561
	LT1	<i>Fagus sylvatica</i>	KC774617	KC774562
	CBS 133207 = LT2*	<i>Fagus sylvatica</i>	KC774618	KC774563
	LT3	<i>Fagus sylvatica</i>	KC774619	KC774564

**DNA extraction and sequencing methods**

The extraction of genomic DNA was performed as reported previously (Voglmayr & Jaklitsch 2011, Jaklitsch et al. 2012) using the DNeasy Plant Mini Kit (QIAGEN GmbH, Hilden, Germany). The partial nuSSU–complete ITS–partial nuLSU rDNA region was amplified with the primers V9G (de Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990). A 1 kb fragment of RNA polymerase II subunit B (*rpb2*) was amplified using the primer pair fRPB2-5f and fRPB2-7cr (Liu et al. 1999). PCR products were purified using an enzymatic PCR cleanup (Werle et al. 1994) as described in Voglmayr & Jaklitsch (2008).

DNA was cycle-sequenced using the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit v. 3.1 (Applied Biosystems, Warrington) and the PCR primers; in addition, the following primers were used: partial nuSSU–complete ITS–partial nuLSU rDNA region: f5.8SF (Jaklitsch & Voglmayr 2011), f5.8SR (Jaklitsch & Voglmayr 2011), ITS4 (White et al. 1990), LR3 (Vilgalys & Hester 1990).



**Fig. 1** Phylogram showing one of eight MP trees 950 steps long revealed by PAUP from an analysis of the nuLSU matrix of selected *Xylariaceae* and *Diatrypaceae*, showing the phylogenetic position of *Lopadostoma* spp., *Barmaelia macrospora*, *Anthostoma decipiens* and *Cryptovalsa rabenhorstii*. MP and ML bootstrap support above 50 % are given at the first and second position, respectively, above or below the branches. Nodes collapsed in the strict consensus of the eight MP trees are marked by asterisks (\*). GenBank accession numbers are given following the taxon names; species sequenced in the present study are formatted in bold. Species labelled in red correspond to *Lopadostoma* s.str.; species labelled in blue are not congeneric with *Lopadostoma*.



### Analysis of sequence data

To reveal the phylogenetic position of *Lopadostoma* within the *Xylariaceae* and to investigate whether the genus is monophyletic, a phylogenetic analysis was performed with nuLSU rDNA (LSU) sequences. Sequences of representative species of *Xylariaceae* and *Diatrypaceae* were selected from GenBank; *Hypocrea rufa* and *Nectria cinnabarina* (*Hypocreales*) were included as outgroup taxa. GenBank accession numbers are given in the phylogenetic tree (Fig. 1). For detailed investigations of species relationships and delimitation within *Lopadostoma*, a combined matrix of nuSSU-ITS1-5.8S-ITS2-LSU rDNA and *rpb2* sequences was produced for phylogenetic analyses, with *Lopadostoma pouzarii* as outgroup according to Fig. 1. The GenBank accession numbers of sequences used in these analyses are given in Table 1.

Sequence alignments for phylogenetic analyses were produced with either MUSCLE v. 3.6 (Edgar 2004) or MAFFT 6.847 (Kato et al. 2002, Kato & Toh 2008) implemented in UGENE 1.10.0 (<http://ugene.unipro.ru>). The resulting alignments were checked using BioEdit v. 7.0.9.0 (Hall 1999). After the exclusion of excessive leading and trailing gap regions and of ambiguously aligned positions, the LSU matrix contained 1 340 characters. The combined data matrix contained 3 342 characters; viz. 2 198 nucleotides of nuSSU-ITS-LSU and 1 144 nucleotides of *rpb2*.

Maximum parsimony (MP) analyses of the nuLSU matrix were performed with PAUP v. 4.0 b10 (Swofford 2002), using 1 000 replicates of heuristic search with random addition of sequences and subsequent TBR branch swapping (MULTREES option in effect, COLLAPSE=MAXBLEN, steepest descent option not in effect). All molecular characters were unordered and given equal weight; analyses were performed with gaps treated as missing data. Bootstrap analysis with 1 000 replicates was performed in the same way, but using 10 rounds of random sequence addition and subsequent TBR branch swapping during each bootstrap replicate; each bootstrap replicate was limited to 1 million rearrangements. The combined matrix was analysed with the same settings, except that COLLAPSE=MINBLEN was implemented.

For ML analyses of both matrices, 1 000 fast bootstrap replicates were computed with RAxML (Stamatakis 2006) as implemented in raxmlGUI 0.95 (Silvestro & Michalak 2012) using the GTRCATI substitution model. Model parameters were calculated separately for the two different gene regions included in the combined analyses.

## RESULTS

### Phylogeny

Of the 1 340 characters in the LSU alignment, 238 were parsimony informative. Fig. 1 shows one of eight MP trees of 950 steps. Tree topology of all eight MP trees was identical except for three minor differences; the three nodes collapsed in the strict consensus tree of the eight MP trees are marked by asterisks in Fig. 1. MP and ML bootstrap support above 50 % are given in Fig. 1 at the first and second position, respectively, above or below the branches.

Of the 3 342 characters in the combined data matrix, 568 were parsimony informative. Fig. 2 shows one of 29 MP trees of 1 552 steps. Tree backbone of all MP trees was identical and topologies differed only within species. MP and ML bootstrap support above 55 % are given in Fig. 2 at the first and second position, respectively, above or below the branches.

In most cases, ITS and *rpb2* sequences were identical or nearly identical within the species, except for *L. meridionale* which showed unusually high intraspecific variation in both genes, which is reflected in long branches within that species (Fig. 2).

Molecular phylogenetic analyses of the nuLSU matrix confirmed monophyly of *Lopadostoma* s.str. with moderate support; sister group relationship to *Creosphaeria sassafras*, which has a similar asexual morph as *Lopadostoma* spp., receives low support. Nodes above this level have no statistical support, therefore conclusions about a relationship of the clade containing this group and the accessions of *Lopadostoma* cf. *polynesium* and *Anthostomella* cf. *conorum* cannot be drawn. *Lopadostoma pouzarii*, *L. cf. amoenum*, *L. cf. polynesium* and *Barrmaelia macrospora* are phylogenetically distinct from *Lopadostoma* s.str. and dispersed among *Xylariaceae* (Fig. 1). *Anthostoma decipiens* and *Cryptovalsa rabenhorstii* are placed within *Diatrypaceae* (Fig. 1).

Molecular phylogenetic analyses of the combined matrix revealed 10 distinct taxa within *Lopadostoma* (Fig. 2), which are recognised at the species level. Of these, *Lopadostoma gastrinum* and *L. turgidum* have already been validly combined; two lineages represent already described taxa, which require formal transfer to *Lopadostoma* (*Phaeosperma dryophilum*, *Sphaeria linosperma*); and six represent yet undescribed species (*L. americanum*, *L. fagi*, *L. insulare*, *L. lechatii*, *L. meridionale* and *L. quercicola*). All species were molecularly highly distinct and received high internal support (Fig. 2). The five *Lopadostoma* species growing on *Quercus* formed an unsupported (Fig. 1) and highly supported (Fig. 2) monophylum in the analyses of the nuLSU and the combined matrices, respectively. *Lopadostoma gastrinum*, *L. lechatii* and *L. linospermum* formed a highly supported clade in both analyses. Morphological characters, such as ascospore size and colour of the entostroma did not correlate with phylogenetic relationships, as e.g. *L. dryophilum* and *L. linospermum*, which are conspicuously similar in these characters, reside in different clades.

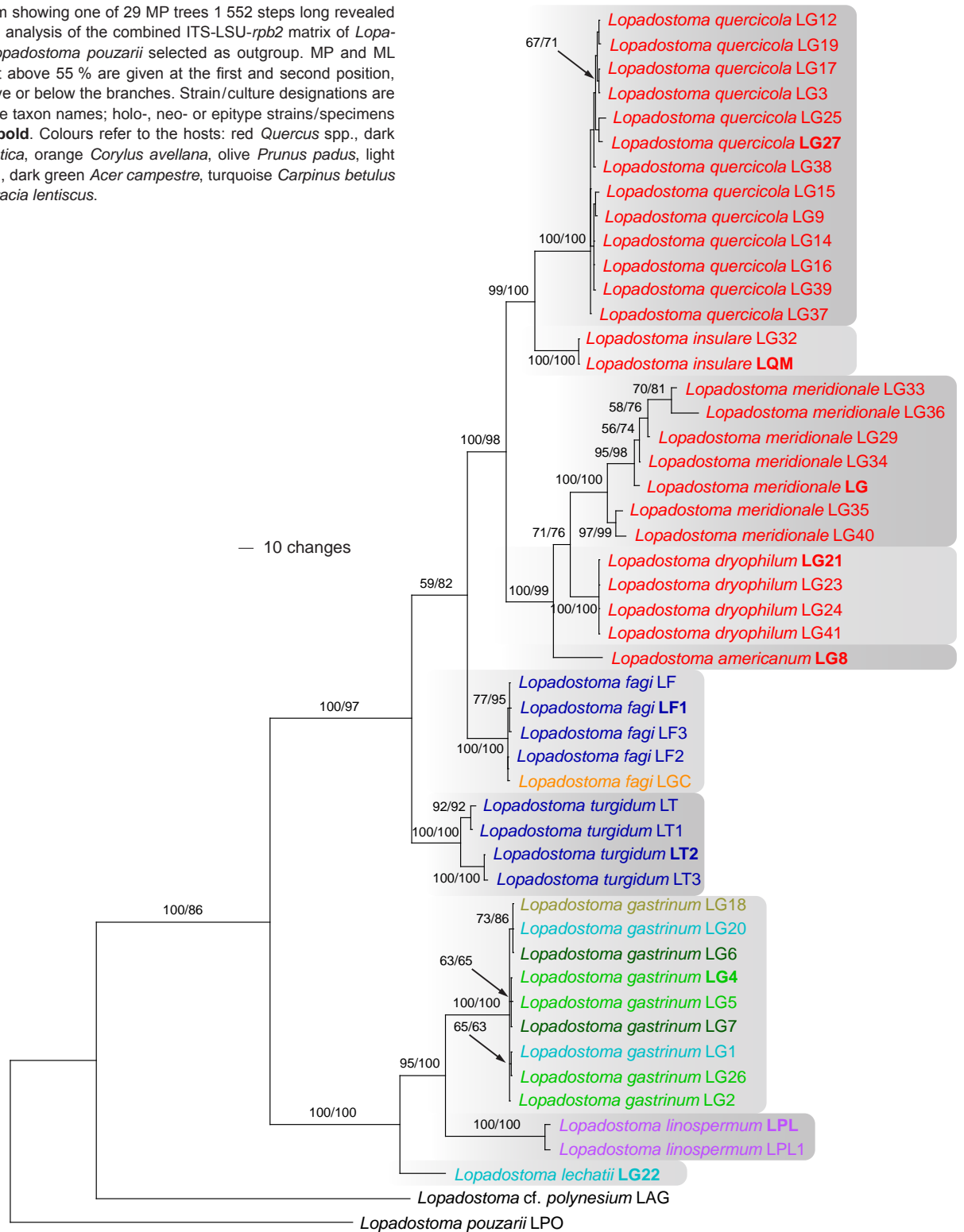
### Phenotype

*Lopadostoma* in a strict sense, i.e. as a monophylum, is highly conserved in sexual and asexual morphology and therefore only two or few species have been recognised, mainly *L. turgidum* on *Fagus* with little morphological variation and *L. gastrinum* on various hosts, with more pronounced variation but no distinct character states that could be recognised as useful for distinction. Most species defined here have stromata that would have been recognised as *L. gastrinum*.

### Sexual morphs

In *Lopadostoma* sexual morphs form pustulate or widely effused stromata, typically immersed in and erumpent from bark, standing on the wood, with only an ectostromatic disc visible or the disc surrounded by blackened bark surface that may be conceived as a clypeus or dorsal stromatic zone; less commonly stromata are superficial on wood after bark disintegration. The ectostromatic disc may be discrete or fused in long bands or lines, circular, elliptic or oblong in outline, even, convex or pulvinate, flush with the bark surface or raised, dark brown, grey or black, smooth or tubercular, with ostioles opening separately in the disc, the latter mostly inconspicuous and umbilicate, sometimes convex, shiny black, or distinctly projecting and cylindrical; varying within species, but with tendencies among species, e.g. ostioles never distinct in *L. turgidum*, usually papillate in *L. dryophilum* and *L. quercicola*, disc tubercular with more or less projecting ostioles in *L. insulare*. Stromata are subglobose to bluntly conical in shape, less commonly widely effused, flat-pulvinate, surrounded by a narrow, black, carbonised encasement, which delimits the stroma from wood and bark. This is seen as a black line in section and referred to it as such in the descriptions below. The entire fungal material encased by the black line is here defined as the stroma. Stroma tissues consist of bark cells mixed with pale-coloured fungal hyphae

**Fig. 2** Phylogram showing one of 29 MP trees 1 552 steps long revealed by PAUP from an analysis of the combined ITS-LSU-*rpb2* matrix of *Lopadostoma*, with *Lopadostoma pouzarii* selected as outgroup. MP and ML bootstrap support above 55 % are given at the first and second position, respectively, above or below the branches. Strain/culture designations are given following the taxon names; holo-, neo- or epitype strains/specimens are formatted in **bold**. Colours refer to the hosts: red *Quercus* spp., dark blue *Fagus sylvatica*, orange *Corylus avellana*, olive *Prunus padus*, light green *Ulmus* spp., dark green *Acer campestre*, turquoise *Carpinus betulus* and lavender *Pistacia lentiscus*.



in lower parts, often appearing mottled, whitish to pale brown; upward, particularly between ostiolar necks the entostroma is often dark or characteristically coloured, e.g. yellow-brown to olivaceous (*L. dryophilum*, *L. linospermum*). The stromata may contain one to many groups of perithecia (part stromata). *Perithecia* are as a rule clustered in valsoid groups, mono-, di- or rarely polystichous, subglobose or flask-shaped and have a dark brown to black wall and short or long more or less convergent ostiolar necks. *Paraphyses* are numerous, long, apically free, 1.5–3.5(–5)  $\mu\text{m}$  wide, little branched. *Asci* are cylindrical, stipitate, with 8 more or less uniseriate ascospores and a globose to ellipsoid *apical apparatus* typically 4–4.5  $\mu\text{m}$  wide, which contains a flat ring-like part blueing in iodine at its

lower end, referred to as *apical ring* in descriptions; the size of the ring is proportional to the ascus size. Length and width of asci and oblique to biseriolate arrangement of ascospores is much dependent on mount preparation, i.e. the pressure applied to separate asci. *Ascospores* are oblong to narrowly ellipsoid, less commonly broadly ellipsoid or banana-shaped, typically symmetrical to slightly inequilateral, unicellular, lack a dwarf cell, are first hyaline, turn pale brown and finally dark to blackish brown at maturity, smooth, have a straight germ slit across the entire spore length present on one side (only in *L. turgidum*) or circumferential (visible as full-length slit on two opposite sides), also when immature; they have usually 2 large guttules, at least when immature; lack a sheath, but a narrow hyaline episporium

c. 0.5 µm wide is sometimes visible in asci. Aberrant ascospores that are very variable in shape are a consequence of aberrant development depending on climatic factors.

**Cultures**

Ascospores of most *Lopadostoma* species germinate slowly on MEA (after few days to several weeks). Growth rates are slow, the colony radius is in the range of 15–20 mm after 1 mo at room temperature, only *L. americanum*, *L. fagi* and *L. insulare* grow slightly faster, while *L. lechatii* reaches less than 10 mm after 1 mo. Colonies of *Lopadostoma* cultures (Fig. 3) start off as flat and white, may develop scant or abundant aerial hyphae and turn yellow, rosy or brown, more pronounced on the reverse. Sometimes brown pigment diffuses through the agar. Most species, albeit not *L. gastrinum* and *L. turgidum*, produce a volatile substance, which becomes noticeable as a strong, unpleasant, varnish-like odour.

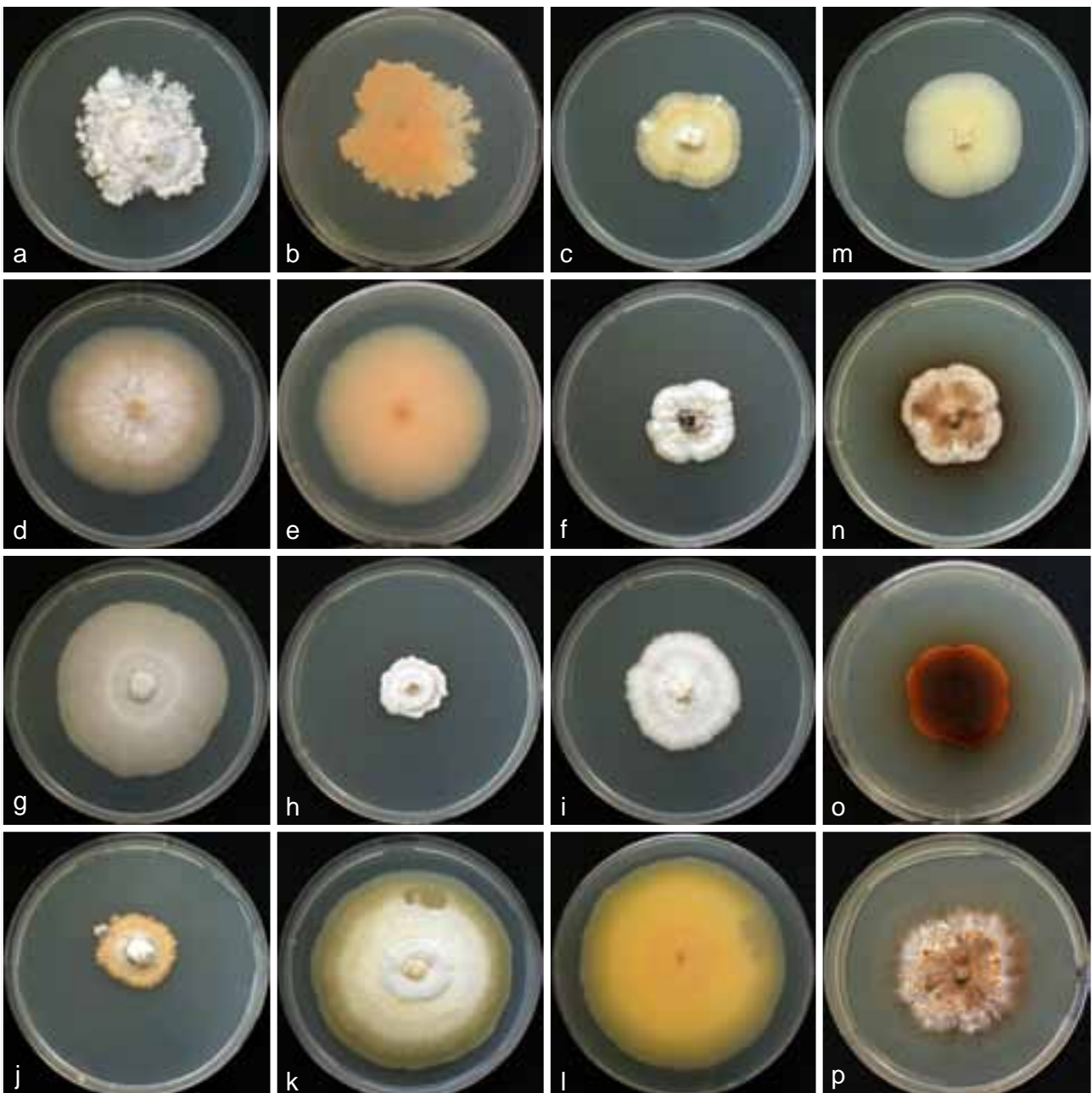
**Asexual morphs**

Libertella-like, only found in the following five species: *L. americanum*, *L. fagi*, *L. linospermum*, *L. meridionale* and *L. turgidum*. Conidia accumulate in yellow, orange, olivaceous or brown to black mucous drops or pycnidia (drops encased by a membrane), they are falcate, unicellular, hyaline, with uniform size among species, but their curvature varies somewhat, in its extreme they are nearly circular (in *L. meridionale*).

**Ecology**

Species of *Lopadostoma* occur exclusively in the bark of trees and shrubs, never immersed in decorticated wood.

Characters useful for distinction and identification of species, in combination: germ slit (on one ascospore side in *L. turgidum*, on both sides in all other species), ascospore size (several species), colour of the entostroma between the ostiolar necks (yellow-brown to olivaceous in *L. dryophilum* and *L. linospermum*, dark brown to black, e.g. in *L. insulare* and *L. meridionale*) and hosts. Strongly and irregularly projecting discs, stromata



**Fig. 3** *Lopadostoma* cultures at room temperature. a, b. *L. americanum* (b. reverse); c. *L. dryophilum* (LG21); d, e. *L. fagi* (LF 1); f. *L. gastrinum* (LG2); g. *L. insulare* (LQM); h. *L. lechatii* (LG22, 61 d); i. *L. linospermum* (LPL); j–l. *L. meridionale* (j. LG; k, l. LG, PDA); m. *L. quercicola* (LG12); n–p. *L. turgidum* (LT2; p. 134 d). All on MEA except k, l. All after 35 d except h and p.



and ostioles are often a consequence of rapidly changing climatic conditions. As an example, a specimen of *L. dryophilum* (LG21) was collected on *Q. petraea* with smooth ectostromatic discs; re-collection from the same branches after heavy rain revealed many irregularly projecting pustules, ejected black spore pustules and variable, aberrant ascospores. Because of considerable overlap of ascospore sizes, the ranges given in the key are mean  $\pm$  standard deviation of at least 30 measurements, excluding minima and maxima. The detailed description of the phenotype above should be consulted before using the key and the individual species descriptions.

## TAXONOMY

### Key to accepted taxa of *Lopadostoma*

1. Stromata widely extended, containing several or many densely gregarious ectostromatic discs; black line absent around individual perithecial clusters; only visible at the periphery of the entire stroma . . . . . 2
1. Stromata well delimited, separate or coalescent in small groups, with a visible black line around them easily observable in transverse and vertical section . . . . . 5
2. Stromata on *Fagus sylvatica* or *Corylus avellana* . . . . . 3
2. Stromata on other hosts . . . . . 4
3. Ascospores 10.2–12.2  $\times$  5.5–6.0  $\mu\text{m}$ , with unilateral germ slit, on *Fagus* . . . . . *L. turgidum*
3. Ascospores 7.7–9.8  $\times$  3.7–4.2  $\mu\text{m}$ , with circumferential germ slit . . . . . *L. fagi*
4. On *Carya alba* in North America, ascospores 9.0–11.8  $\times$  4.0–4.7  $\mu\text{m}$  . . . . . *L. juglandinum*
4. Stromata on *Quercus* spp. in Europe, ascospores 9.5–12.0  $\times$  4.3–5.0  $\mu\text{m}$  . . . . . *L. quercicola*
5. Stromata internally white to pale-coloured, especially between ostiolar necks . . . . . 6
5. Stromata internally darker-coloured, olivaceous, brown to blackish between ostiolar necks . . . . . 7
6. Ascospores 10.5–12.8  $\times$  4.5–5.5  $\mu\text{m}$ ; on *Ulmus* and other hosts but not *Fagus* or *Quercus* . . . . . *L. gastrinum*
6. Ascospores 8.0–9.5  $\times$  3.5–4.3  $\mu\text{m}$ ; on *Carpinus betulus* . . . . . *L. lechatii*
7. Tissue between ostiolar necks yellow-brown or olivaceous, ascospores large, (12–)13–17.5  $\times$  4.3–6.2  $\mu\text{m}$  . . . . . 8
7. Tissue between ostiolar necks dark brown, dark grey to blackish; ascospores smaller; on *Quercus* spp. . . . . 10
8. On *Quercus petraea* and *Q. robur* in temperate Europe . . . . . *L. dryophilum*
8. Not on *Quercus* . . . . . 9
9. On *Pistacia lentiscus* in Mediterranean Europe and North Africa . . . . . *L. linospermum*
9. On *Ailanthus*, known from a single collection in Switzerland; ascospores 12–15  $\times$  4.3–5.5  $\mu\text{m}$  (colour of tissue between ostioles to be verified) . . . . . *L. ailanthi*
10. Ascospores 7.2–9.2  $\times$  3.5–4.0  $\mu\text{m}$ , on *Quercus coccifera* and *Q. ilex* on Mediterranean islands . . . . . *L. insulare*
10. Ascospores averaging larger, 9.2–12.8  $\times$  3.5–5.0  $\mu\text{m}$  . . . . . 11
11. On white oaks, e.g. *Quercus alba*, in North America; ascospores 9.2–11.5  $\times$  3.5–4.2  $\mu\text{m}$  . . . . . *L. americanum*
11. On other species of *Quercus*, in Europe . . . . . 12
12. On *Quercus coccifera* and *Q. ilex*; ostioles umbilicate in the disc; ascospores 10.3–12.8  $\times$  4.0–4.8  $\mu\text{m}$ ; forming a libertella-like asexual morph in culture . . . . . *L. meridionale*
12. On *Quercus cerris*, *Q. petraea*, *Q. pubescens* and *Q. suber*, possibly also *Q. robur*; ostioles typically papillate; ascospores 9.5–12.0  $\times$  4.3–5.0  $\mu\text{m}$ ; not forming an asexual morph in culture . . . . . *L. quercicola*

## SPECIES DESCRIPTIONS

Descriptions of accepted species are given in alphabetical order.

***Lopadostoma ailanthi*** (G.H. Otth) Jaklitsch, J. Fourn. & Voglmayr, *comb. nov.* — MycoBank MB803802; Fig. 4a–e

*Basionym.* *Phaeosperma ailanthi* G.H. Otth (as *P. ailanthi* (Otth) Nke.), Mitth. Naturf. Ges. Bern 1870: 101. 1870.

*Holotype.* SWITZERLAND, Bern, Thun, near Steffisburg, in a garden, on a dead twig of *Ailanthus altissima* (given as *Ailanthus glandulosa*), without date, G.H. Otth, Nr. 51 (B).

*Stromata* immersed in bark, subglobose, c. 3 mm diam and 2.5 mm high, appearing on the bark surface as a circular or elliptic black ectostromatic disc up to 2.8  $\times$  1.4 mm, compact, surrounded by a black line. Tissue within the black line dark brown to black. *Perithecia* monostichous or distichous, c. 1 mm high, 0.5–0.8 mm diam; ostiolar necks long, convergent in the disc. *Asci* cylindrical, containing 8 uniseriate ascospores, apical ring flat, amyloid, (1.8–)2–2.3(–2.5)  $\mu\text{m}$  wide and (0.4–)0.6–0.9  $\mu\text{m}$  high (n = 15). *Ascospores* oblong or narrowly ellipsoid, (10.5–)11.7–15.0(–16.5)  $\times$  (4.0–)4.3–5.5(–6.0)  $\mu\text{m}$ , l/w (2.1–)2.4–3.2(–4.2) (n = 33), dark brown, smooth, not or only slightly compressed, germ slit circumferential, straight.

*Distribution & Habitat* — Switzerland, in corticated branch of *Ailanthus altissima*; only known from the type specimen.

*Notes* — Otth (1870) described this taxon as *Phaeosperma ailanthi* (Otth) Nke. after Nitschke had told him in a letter that it belongs to *Phaeosperma*. However, the correct citation is *Phaeosperma ailanthi* G.H. Otth. Nitschke's impact could be honoured as *Phaeosperma ailanthi* Nitschke ex G.H. Otth, which is not necessary. On the label of the type specimen Otth also wrote the names *Anthostoma ailanthi* Otth and *Diatrype ailanthi* Otth. These names have never been published, but Saccardo (1895: 25) included the name *Anthostoma ailanthi* (Otth) Nke. in Otth, apparently as his own interpretation.

This fungus is clearly a species of *Lopadostoma*; however, in the absence of DNA data its status as a species distinct from *L. dryophilum* is preliminary, because the type material is scant, consisting only of two halves of mostly effete stromata, which are infested by *Eurotium herbariorum*. The wood is lightweight, pale-coloured and ring-pored, which confirms *Ailanthus*. *Lopadostoma dryophilum*, which has a similar ascospore size, occurs in the same area. Recent attempts to find *L. ailanthi* have been without success.

***Lopadostoma americanum*** Jaklitsch, J. Fourn., J.D. Rogers & Voglmayr, *sp. nov.* — MycoBank MB803803; Fig. 5

= *Anthostoma dryophilum* (Curr.) Sacc. sensu Ellis & Everhart (1892).

*Holotype.* USA, West Virginia, Upshur Co., Audra State Park, on corticated branch of *Quercus* sp. (white oak), 29 Aug. 2008, J.D. Rogers (WU 32033, ex-type culture CBS 133211 = LG8).

*Etymology.* Occurring in America.

*Ectostromatic discs* flat or convex, often ill-defined, circular or ellipsoid in outline, 0.7–1 mm in their greatest dimension, projecting to 0.3 mm above the host surface, roughened, carbonaceous, shiny in places; ostioles opening separately in the disc, inconspicuous, umbilicate. *Stromata* for the most part immersed in bark, pustulate-erumpent, separate, scattered, rarely in contact, subglobose, 2–3 mm diam, delimited from surrounding bark by a black carbonized line; the latter 80–120  $\mu\text{m}$  thick, irregular in outline, reaching the wood surface and spreading over it between adjacent stromata. Tissue between ostiolar necks dark yellow-brown, grey to black, woody; tissue around and



**Fig. 4** a–e: *Lopadostoma ailanthi* (holotype). a. Ectostromatic disc; b. vertical stroma section; c, d. apical ascus rings in Lugol; e. ascospores showing germ slit (both sides visible in one spore). — f–s: *Lopadostoma juglandinum*. f–i. Ectostromatic discs (f. showing discoid ostioles; g. var. *caryae*; h. distinct ostioles in pale brown disc); j, k. vertical stroma sections; l–o. asci (o. in Lugol); p. ascospores showing germ slit; q, r. apical ascus rings in Lugol; s. ascospores (f, h–l, n–p, r. holotype F1318238; g. var. *caryae* K(M) 177255; m. var. *caryae* from NY; q, s. K(M) 177254). — Scale bars: a = 0.5 mm; b, f, j, k = 0.8 mm; c, d = 7  $\mu$ m; e, p, q, s = 5  $\mu$ m; g = 2.2 mm; h, i = 0.3 mm; l–o, r = 10  $\mu$ m.

beneath the perithecia composed of brownish, scarcely altered bark tissue, in places mixed with whitish mycelium. *Perithecia* 6–15 per stroma, arranged in valsoid configuration, monostichous in smaller stromata, polystichous in larger ones, subglobose to ovoid, often laterally compressed, 0.4–0.9 mm diam, with long ostiolar necks converging toward the ectostromatic disc. *Asci* cylindrical, with 8 uniseriate ascospores, spore part

(50–)55–70(–81)  $\times$  (5.0–)6.0–7.5(–8.3)  $\mu$ m (n = 34), sometimes fusiform due to partly overlapping biseriate or oblique ascospores, flat amyloid apical ring (1.3–)1.5–1.8(–2.0)  $\mu$ m diam, 0.5–0.7(–0.8)  $\mu$ m high (n = 35); stipe up to nearly as long as the spore part. *Ascospores* oblong to narrowly ellipsoid, (8.2–)9.2–11.5(–13.7)  $\times$  (3.3–)3.5–4.2(–4.7)  $\mu$ m, l/w (1.9–)2.3–3.0(–3.6) (n = 62), dark to blackish brown, smooth,



with 2 guttules when young, with commonly visible, straight, circumferential germ slit.

Cultures and asexual morph — On MEA after 35 d at room temperature colony radius 19–29 mm (to 36 mm after 4.5 mo). Colony typically with angular or irregular outline; margin colourless, diffuse; colony surface thick, white, covered by highly variable tufts or pustules of aerial hyphae; colony reverse rosy with yellow tone; odour none to unpleasant. Conidia forming after c. 55 d at room temperature in mucous, initially hyaline drops c. 0.7–1 mm diam that turn yellowish, after 2 mo olivaceous

and eventually black. Asexual morph (on MEA after 68 d at 25 °C) libertella-like. Conidia falcate, (17–)18.5–22.5(–24.5) × (1.1–)1.2–1.5 μm, l/w (13–)14–17(–19) (n = 30), hyaline, 1-celled, smooth, upper end subacute, base truncate, curved to nearly semicircular. Growth on PDA slightly faster than on MEA; colony nearly circular, with uneven white mat, colourless, white to yellowish margin, and yellowish reverse; after > 1 mo forming large thick yellowish pustules but no conidial drops.

Distribution & Habitat — North America, on *Quercus* spp. (white oaks).



**Fig. 5** *Lopadostoma americanum* (WU 32033, culture LG8). a–o. Sexual morph: a. surface view of stromata; b. ectostromatic disc; c, d. transverse sections of a stroma (c. ostiolar level; d. perithecial level); e, f. vertical sections of a stroma; g–l. ascospores (l. showing germ slit); j, k. apical ring in Lugol; m–o. asci (o. in Lugol). — p–u. Cultures and asexual morph: p. colony (64 d); q. conidial drops (68 d); r–u. conidia (68 d) (p–u: all on MEA at 25 °C). — Scale bars: a = 1 mm; b–e = 0.5 mm; f = 0.3 mm; g–l = 3 μm; m, n = 10 μm; o, s, t = 7 μm; q = 0.2 mm; r = 15 μm; u = 5 μm.

*Other specimen examined.* USA, New Jersey, Gloucester County, Newfield, on dead limbs of *Quercus alba*, 11 Oct. 1891, R.A. Harper, N.A.F. (without number; NY).

**Notes** — The only available material that yielded a culture (WU 32033) contains mostly cut or depauperate stromata. The dimensions do probably not reflect the entire variation range that can be expected. Morphologically, *L. americanum* is similar to other species on *Quercus* with dark stroma tissues between the ostioles. It is one of the few species on *Quercus* that produces an asexual morph on MEA. Unlike other species of *Lopadostoma*, the conidial drops turn olivaceous and eventually black.

We establish here the new name *L. americanum* for material that J.B. Ellis (see Ellis & Everhart 1892: 581) erroneously called *Anthostoma dryophilum* (Curr.) Sacc. The latter name was based on *Sphaeria dryophila* Curr., which was established on a British specimen collected by Hooker in Weybridge, Surrey and has distinctly larger ascospores than *L. americanum*. *Anthostoma dryophilum* (Curr.) Sacc. var. *minor* Cke. (1876; Grevillea V, p. 32, pl. 75/13 as *Diatrype dryophila* var. *minor*), may however be a different species of *Lopadostoma*, particularly due to the different hosts of the red oak group (*Quercus coccinea*, *Q. nigra*). Morphologically, it is similar to *L. americanum*, but differs in more effused, widely erumpent but less prominent compound stromata, which are covered by blackened epidermis. Several or many minute, ill-defined, tubercular discs 0.2–0.7 mm diam per compound stroma split the bark irregularly; individual stromata contain 6–15 perithecia and the internal tissues are dark brown. The spore part of asci measure (61–)66–82(–84) × (5.3–)5.7–7.6(–8.3) µm (n = 10), and the ascospores (8.3–)9.5–12.2(–14.0) × (3.5–)3.8–4.5(–5.2) µm, l/w (2.0–)2.3–2.9(–3.3) (n = 30), slightly lighter and more reddish brown than in *L. americanum* and partly nearly rhomboid. Asci are only slightly longer than in *L. americanum* and stroma features vary considerably among specimens, therefore only DNA data of freshly collected specimens would provide certainty whether or not these forms represent different species. Several specimens of *Anthostoma dryophilum* var. *minor* of the Ellis Collection are housed in NY, all from New Jersey, Gloucester County, Newfield, on bark of *Quercus coccinea*, no date given; type of *A. dryophilum* var. *minor* (N.A.F. 87; no other information); same locality, from 22 May 1893.

***Lopadostoma dryophilum*** (G.H. Otth) Jaklitsch, J. Fourn. & Voglmayr, *comb. nov.* — MycoBank MB 803804; Fig. 6

*Basionym.* *Phaeosperma dryophilum* G.H. Otth, Mitt. Naturf. Ges. Bern Nr. 654–683: 42. 1868.

= *Sphaeria* (*Diatrype*) *dryophila* Curr., Trans. Linn. Soc. London 22: 269. 1859 [non *Sphaeria dryophila* Schwein., Trans. Amer. Philos. Soc., Ser. 2, 4, 2: 226. 1832.

= *Anthostoma dryophilum* (Curr.) Sacc., Syll. Fung. 1: 308. 1882.

= *Lopadostoma morthieri* (Fuckel) Schrantz, Bull. Trimestriel Soc. Mycol. France 76: 370. 1960 (publ. 1961).

= *Quaternaria morthieri* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 229. 1870 (1869–1870).

*Holotype* of the basionym *Phaeosperma dryophilum*. SWITZERLAND, Bern, Bremgartenwald, on *Quercus* sp. (*Q. petraea* or *Q. robur*), no date given, (B 70 0014745; as *Valsa tumida*). Epitype here designated: AUSTRIA, Niederösterreich, Gießhübl-Perchtoldsdorf, on branches of *Quercus petraea*, soc. old *Diatrypella quercina* and *Enchnoa infernalis*, 25 Mar. 2012, H. Voglmayr (WU 32035; ex-epitype culture CBS 133213 = LG21; MBT175915).

*Ectostromatic discs* dark brown, grey to black, flat, slightly convex or concave, often surrounded by typically darkened, ruptured, grey periderm, sometimes in stellate manner, 0.4–3 mm in their greatest dimension, often coalescent in small groups or several scattered on a common, slightly convex, pulvinate stroma, projecting 0.3–1.6 mm above the host surface, circular or elliptic in outline, smooth to roughened, often with slightly

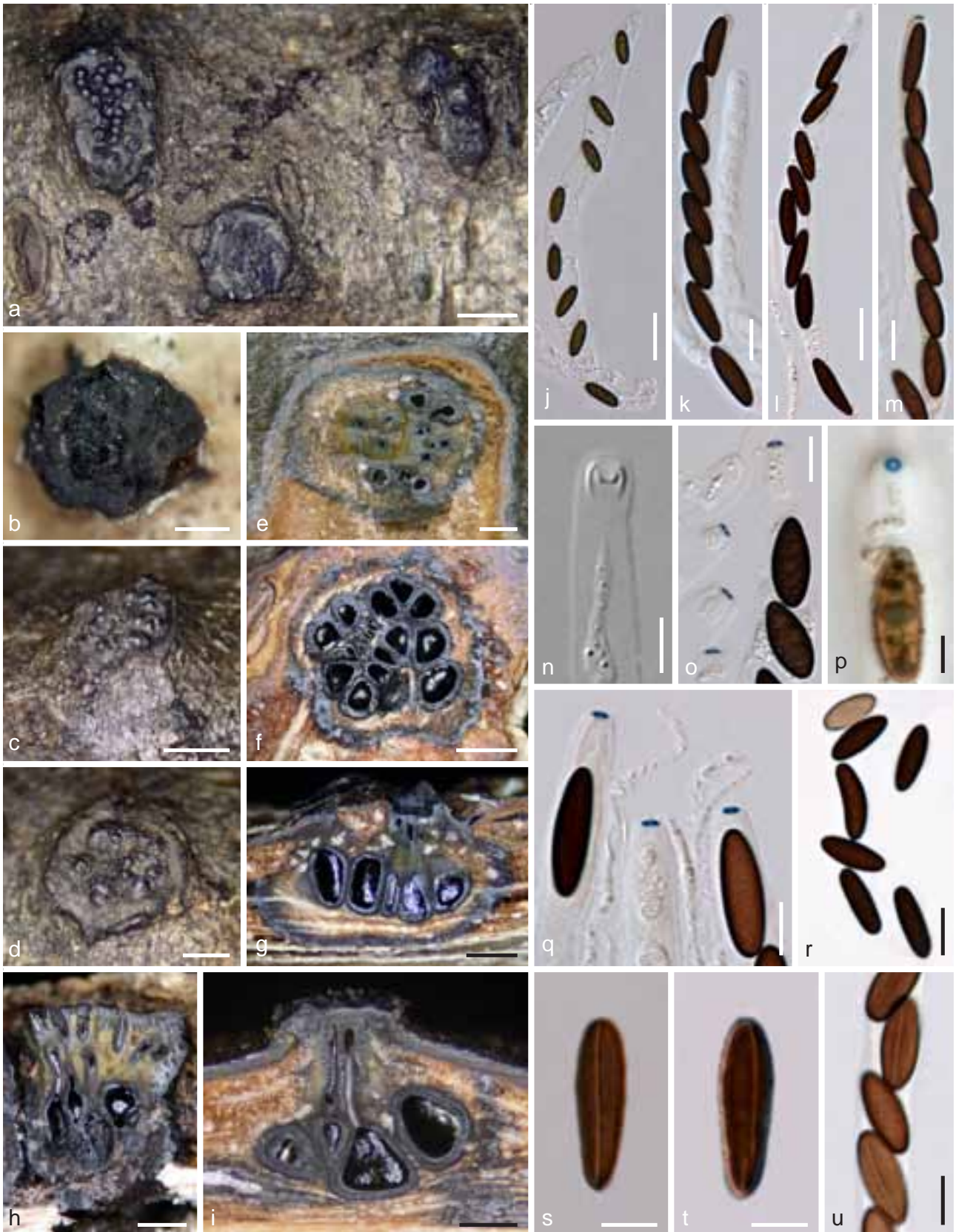
projecting black ostioles. *Ostioles* opening separately in the disc, inconspicuous or raised and bluntly rounded 80–120 µm high, 50–220 µm diam. *Stromata* (part stromata in case of widely effused entire stromata) pustulate, erumpent through the bark, subglobose, 2–6 mm wide, 1–2.6 mm high, surrounded by a black stromatic line, the latter 100–200 µm thick, irregular in outline, reaching the wood surface and spreading over it between adjacent stromata or more commonly spreading widely and encompassing several coalescent stromata. Tissue between ostiolar necks typically distinctly yellow-brown to olivaceous, at times weakly developed, woody, not releasing pigment in 10 % KOH; tissue around and beneath perithecia brownish, composed of bark tissue mixed with white fungal tissue in variable proportions, at times of hardly altered bark and compact, rarely blackish brown. *Perithecia* 2–25 per stroma, arranged in valsoid configuration, monostichous in smaller stromata, polystichous in larger ones, subglobose or flask-shaped, 0.3–1 mm diam, somewhat laterally compressed when crowded, with short to long ostiolar necks converging toward the disc. *Asci* long cylindrical, variably stipitate, containing (6–)8 uniseriate, sometimes partly biseriate or obliquely overlapping ascospores, spore part (90–)98–120(–126) × (6–)7–10(–13) µm (n = 47); apical ring flat, amyloid, refractive in 3 % KOH, (2.0–)2.2–2.5(–3.0) µm wide and (0.5–)0.6–0.9(–1.2) µm high (n = 54); asci longer and broader in water than in 3 % KOH. *Ascospores* (10–)13–17.5(–20) × (3.3–)4.5–5.5(–6.3) µm, l/w = (1.9–)2.6–3.6(–5.3) (n = 210), oblong, narrowly ellipsoid or narrowly fusiform, unicellular, dark brown to nearly black, equi- to slightly inequilateral or slightly curved (nearly banana-shaped), not compressed, with straight, circumferential germ slit and 2 large and sometimes several small guttules (in water and KOH).

*Cultures and asexual morph* — On MEA after 35 d at room temperature colony radius 18–20 mm (after 4.5 mo centrally inoculated plate nearly entirely covered). Colony typically circular, thin, first with cottony aerial hyphae, soon flattening and inconspicuous; surface and reverse distinctly yellow to pale orange, often with a rosy tone, reverse more intensely coloured; sometimes turning dull olive-brown from the centre; margin often lighter or white, well-defined, sometimes slightly lobed; odour fruity or unpleasant, ‘chemical’, varnish-like; in the latter case growth often stopping soon. No conidia detected within 4.5 mo. Growth on PDA slightly faster than on MEA; colony surface white by aerial hyphae, turning pale brown from the centre; reverse dull yellow, hard brownish pustules but no conidia formed.

*Distribution & Habitat* — Europe, in corticated branches of *Quercus petraea* and probably *Q. robur*; apparently more common in Western Europe.

*Other specimens examined.* FRANCE, Ariège, Rimont, Las Muros, on branch of *Quercus petraea*, 30 Aug. 2009, J. Fournier JF 09233 (WU 32034; culture LG11); *ibid.*, same host, 25 Mar. 2012, J. Fournier JF 12038 (WU 32037; culture LG24); Rimont, trail from Grillou to Sourroque, on branch of *Quercus petraea*, 13 Mar. 2012, J. Fournier JF 12029 (WU 32036; culture LG23); Rimont, Saurine, elev. c. 450 m, on bark of *Quercus petraea*, 21 Nov. 2008, J. Fournier JF 08196; Pyrénées-Atlantiques, Oloron, Préchacq-Josbaig, Bois de Josbaig, *Quercus* cf. *petraea*. — GERMANY, Hessen, Oestrich, Vorderwald, no date given, Fuckel, on branch of *Quercus petraea* (G 00111565, as *Quaternaria morthieri*). — SPAIN, Asturias, Soto de Los Infantes, near Viescas, on branches of *Quercus petraea*, W. Jaklitsch & H. Voglmayr (WU 32097). — SWITZERLAND, Jura mountains, near Neuchatel, on branch of *Quercus* cf. *petraea*, 28 Apr. 1867, P. Morthier, teste G. Colomb-Duplan (G 00111566, as *Quaternaria morthieri*, lectotype of *Q. morthieri* here selected; MBT175914); *ibid.*, 15 Nov. 1867, P. Morthier (G 00111563, as *Quaternaria morthieri*); *ibid.*, Mar. 1871 (G 00111564, as *Quaternaria morthieri*). — UNITED KINGDOM, Surrey, Weybridge, on decaying branches of *Quercus* sp. (probably *Q. robur*, Sept. 1856, ex herb. F. Currey (K(M) 177257, holotype of *Sphaeria dryophila*, given as the unpublished name *Valsa dryophila* Curr. on the label); no locality given, Feb. 1939, C.G.C. Chesters (only culture CBS 107.39 = LG41 sequenced).





**Fig. 6** *Lopadostoma dryophilum*. a–d. Ectostromatic discs; e, f. transverse stroma section (e. ostiolar level; f. perithecial level); g–i. vertical stroma sections; j–m. asci (j. fresh, in water; m. in Lugol); n–q. apical ascus rings (o–q. in Lugol); r. ascospores; s–u. ascospores showing germ slit (s, t. germ slit on both sides of the same ascospore) (a, c, d, e, i, j, l, n–p, s, t: LG21; b, k, m: holotype of *Sphaeria dryophila* K(M) 177257; f–h: JF08196; q, u: lectotype of *L. morthieri* G 00111563; r: holotype of *P. dryophilum*). — Scale bars: a, c, f = 1 mm; b, d, e, i = 0.5 mm; g, h = 0.8 mm; j, l = 15 µm; k, m, r = 10 µm; n, p, s, t = 5 µm; o, q, u = 7 µm.



Notes — Diagnostic of *L. dryophilum* are the large asci and ascospores as well as the distinctly yellow-brown to olivaceous entostroma between ostiolar necks, which is similar to *L. lino-spermum* on *Pistacia lentiscus*. In overmature material this tissue may be dark brown. The black stromatic line is usually conspicuous around individual stromata but may sometimes be overlooked when only present around widely effused stromata that contain several perithecial groups.

Comments to the selection of the basionym: *Phaeosperma dryophilum* G.H. Otth is the basionym of *L. dryophilum*. Otth (1868) attributed the taxon to Nitschke, because the latter had told him about the possible generic affiliation of the fungus. However, there is no indication that Nitschke provided a diagnosis, therefore a more complete but long and unnecessary citation would be *Phaeosperma dryophilum* Nitschke ex G.H. Otth. As addressed by Otth (1868: 42) he had misidentified the fungus in 1863 (Otth 1863: 79) as *Valsa tumida* and deposited the type material under this name. *Sphaeria (Diatrype) dryophila* Curr. (1859) is older than *P. dryophilum*, but a later homonym of *Sphaeria dryophila* Schwein. (1832), a fungus described from leaves, i.e. not representing a *Lopadostoma*. Currey (1859) described the fungus as a *Sphaeria* and put the name *Diatrype* in parentheses to relate it to the system of Fries' Summa Vegetabilium Scandinaviae, while he obviously did not accept at that time of splitting *Sphaeria* into separate genera by Fries and other authors, explicitly writing on page 261: "In the Summa Vegetabilium Scandinaviae the *Sphaeriae* included in the above divisions are thrown into distinct genera...". He preferred to maintain the large genus *Sphaeria* with several sections and divisions. Saccardo (1882: 308) ignored Currey's intentions and the generic name *Sphaeria*, but simply cited the name as *Diatrype dryophila* Curr. and combined it as *Anthostoma dryophilum* (Curr.) Sacc. Index Fungorum took up this name as *Anthostoma dryophilum* Sacc. (1882), defining *Sphaeria dryophila* Curr. 1859 as a replaced synonym. However, *Phaeosperma dryophilum* G.H. Otth (1868) is older than *Anthostoma dryophilum* Sacc. (1882) and therefore the valid basionym of *L. dryophilum*. The name *Anthostoma dryophilum* (Curr.) Sacc. was only rarely used in Europe, but erroneously by J.B. Ellis for a different fungus in North America (see above under *L. americanum*).

***Lopadostoma fagi* Jaklitsch, J. Fourn. & Voglmayr, sp. nov.**  
— MycoBank MB803805; Fig. 7

*Holotype*. AUSTRIA, Niederösterreich, Mauerbach, on a corticated branch of *Fagus sylvatica*, 13 June 2011, W. Jaklitsch (WU 32039; ex-type culture CBS 133206 = LF1).

*Etymology*. For its occurrence on *Fagus*.

*Stromata* widely effused on recently dead branches, up to 30–40 cm long, uniting numerous small, typically densely gregarious, separate or coalescent, flattened pustules 1–2 mm diam, slightly raising the periderm, discolouring it dark silvery grey above the pustules, contrasting with the surrounding reddish brown colour. *Pustules* pierced at their centre by a dull black ectostromatic disc 0.37–0.84 mm in its greatest dimension (av. = 0.53 mm, n = 90), circular or elliptic, flat, slightly convex or concave, projecting 120–250 µm above the periderm, surrounded by teeth-like remnants of the ruptured periderm, sometimes containing distinctly papillate ostioles. Tissue between the ostioles blackish, soft-textured, tissue surrounding perithecia somewhat powdery, composed of white fungal tissue mixed with yellowish brown bark cells; tissue beneath the perithecia compact, composed of nearly unaltered bark, delimited in the lower part by a thin, often inconspicuous, dark

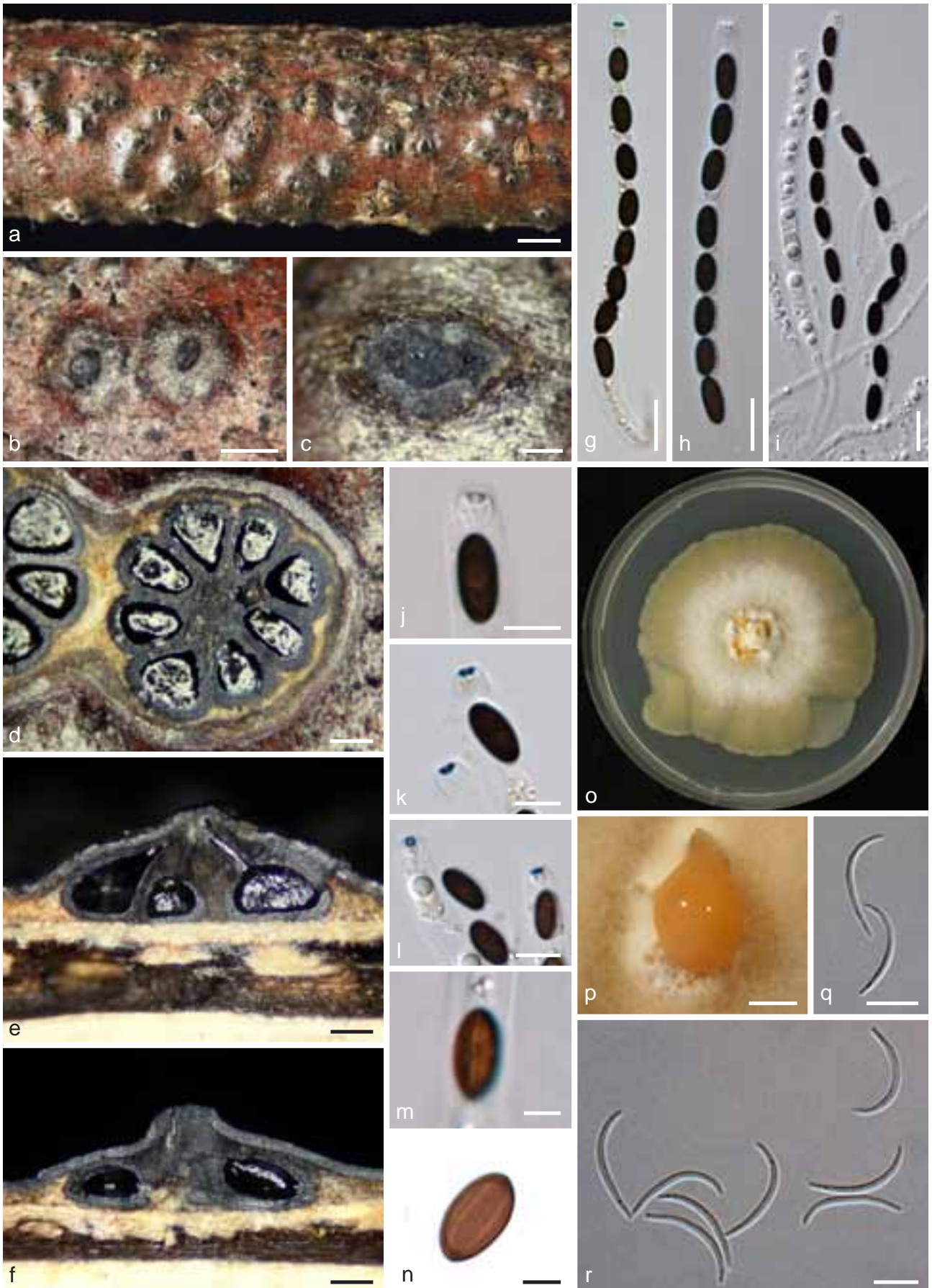
brown to black stromatic line; loosening bark below stromata seated on a thick dark brown felty layer spreading over the wood surface. *Perithecia* (3–)6–8 in a cluster, monostichous, circinate, flask-shaped or depressed-globose, at the periphery inclined toward the centre, 250–750 µm high, 330–620 µm wide, with long ostiolar necks converging toward the disc, opening separately in the disc. *Ostiolar openings* umbilicate, inconspicuous. *Asci* cylindrical, spore-bearing part (53–)64–79(–83) × (5.0–)5.3–6.0(–7.0) µm (n = 31), with 8 uniseriate ascospores; apical ring (1.6–)1.9–2.2(–2.5) µm wide, (0.6–)0.7–1.1(–1.3) µm high (n = 35). *Ascospores* oblong or narrowly ellipsoid, (6.5–)7.7–9.8(–11.8) × (3.2–)3.7–4.2(–4.8) µm, l/w (1.4–)1.9–2.5(–2.9) (n = 121), unicellular, blackish brown, smooth, with a circumferential, straight germ slit, with 2 large guttules, at least when immature.

Cultures and asexual morph — Ascospores germinating slowly (after 1–4 wk on 2 % MEA). On MEA after 35 d at room temperature colony radius c. 25 mm (c. 40 mm after 2 mo; colony entirely covering a centrally inoculated plate after c. 4 mo); colony circular with well-defined margin, first white, covered by a variable white mat or tufts of aerial hyphae, turning rosy, particularly at the margin and on the reverse, sometimes mixed with yellow; odour indistinct to slightly strongly 'chemical', varnish-like (isolate LGC). Conidia forming after 1–2 mo in yellow to orange mucous drops to c. 3 mm diam, falcate, (18–)19–23(–27) × 1.4–1.7 µm, l/w (11.5–)13–15.7(–17.6) (n = 30), unicellular, hyaline, with acute upper end and narrowly truncate lower end. On PDA colony similar, less rosy, more yellow, sometimes aerial hyphae forming white tufts or pustules around the plug or grey or brown spots appearing in the centre. Conidia formed after 48 d at room temperature in orange conidial drops (0.3–)0.8–2 mm diam in the colony centre, eventually (after 4–5 mo) turning to large mucous brown pustules.

Distribution & Habitat — Europe, in corticated branches of *Fagus sylvatica*; common on this host; found once on *Corylus avellana*.

*Otherspecimens examined* (all on corticated branches of *Fagus sylvatica* except where noted). AUSTRIA, Kärnten, St. Margareten im Rosental, grid square 9452/4, Stariwald, 8 June 1992, W. Jaklitsch W.J. 30 (WU 32099); Zabrd, 16 Aug. 1996, W. Jaklitsch W.J. 923 (WU 32100); Niederösterreich, Hainbuch, grid square 7763/1, 28 Sept. 1996, W. Jaklitsch; Mauerbach, grid square 7762/4, 16 May 1992, W. Jaklitsch W.J. 25 (WU 32098); Weidlingbach, 3 Mar. 2012, W. Jaklitsch & H. Voglmayr (WU 32041; culture LF3); Steiermark, Berghausen, Graßnitzberg, grid square 9259/4, 20 Sept. 1996; Klösch, Koglwald, grid square 9261/2, 17 Sept. 1996 (GZU), W. Jaklitsch; Mönichkirchen, Tränktörl-Glashütte, 1 Aug. 2010, W. Jaklitsch (WU 32038; culture LF); Pöllau, Schönauklamm, grid square 8760/2, 12 Sept. 2002, W. Jaklitsch. — FRANCE, Ariège, Rimont, 1.5 km from the village on the road D18, 14 Nov. 2011, J. Fournier JF 11169 (WU 32040; culture LF2). — GERMANY, Hessen, NW Schifferberg, grid square 5418/1, elev. 210 m, soc. *Biscogniauxia marginata*, 31 Mar. 2007, W. Schöbner, comm. K. Siepe SI 10/2007 (WU 32042). — UNITED KINGDOM, England, Yorkshire, Worksop, Rotherham, Anston, Anstonstones Wood, on a corticated branch of *Corylus avellana*, 16 May 2011, W. Jaklitsch (WU 32043; culture LGC).

Notes — Stromata of *L. fagi* are similar to those of *L. turgidum*, but differ in slightly larger ectostromatic discs that may contain distinctly papillate ostioles, smaller, particularly narrower ascospores, a circumferential germ slit, slow germination and rosy colour of colonies on MEA. Both species often occur in the same beech forest and are indistinguishable in the field. The only specimen found on *Corylus* yielded slightly deviant sequences and a stronger odour in MEA cultures. Vasilyeva & Scheuer (1996), who already noticed the circumferential germ slit, reported this species as *Lopadostoma* sp. from six localities in Austria.



**Fig. 7** *Lopadostoma fagi*. a–n. Sexual morph: a. panoramic view of stromata; b. two stromata in face view; c. ectostromatic disc; d. transverse stroma section; e, f. vertical stroma sections; g–i. asci (g. in Lugol); j–l. apical ring (k, l. in Lugol); m, n. ascospores showing germ slit (n. compressed, showing circumferential germ slit). — o–r. Cultures and asexual morph: o. colony on PDA (RT, 55 d); p. conidial drop; q, r. conidia (p–r: all on MEA at 25 °C after 48 d. a–f, i, l, m, p–r: LF; g, h, j, k, n, o: LF2). — Scale bars: a = 1.5 mm; b, p = 1 mm; c, e, f = 0.2 mm; d = 0.3 mm; g–i, q, r = 10 µm; j, k = 5 µm; l = 7 µm; m, n = 3 µm.





**Fig. 8** *Lopadostoma gastrinum*. a–d. Ectostromatic discs; e. superficial stroma with projecting ostioles; f, g. transverse stroma sections (f. ostiolar level); h–j. vertical stroma sections; k–m. asci; n. ascospores laterally collapsing in lactic acid; o, p. ascospores showing germ slit; q, r. apical ascus ring in Lugol; s. colony on MEA at 25 °C after 63 d (a: LG7; b, f, g, i: LG5; c, j: LG20; d, s: LG26; e, l, m: LG6; h: JF12024; k, o, p: LG2; n, q, r: LG4). — Scale bars: a = 1.5 mm; b, c, f, g, j = 0.5 mm; d = 0.2 mm; e, i = 1 mm; h = 2 mm; k–n = 10 µm; o–r = 5 µm.

***Lopadostoma gastrinum*** (Fr.) Traverso, Fl. Ital. Crypt. 2, 1: 169. 1906. — Fig. 8

*Basionym.* *Sphaeria gastrina* Fr., Syst. Mycol. (Lundae) 2, 2: 379. 1823.  
= *Anthostoma gastrinum* (Fr.) Sacc., Atti Soc. Veneto-Trentino Sci. Nat. Padova 2: 143. 1873.

? = *Lopadostoma formosum* (Ellis & Everh.) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

*Neotype proposed here.* ITALY, Lombardia, Brescia, Sopraponte, on branch of *Ulmus minor*, 21 Oct. 2011, W. Jaklitsch (WU 32046; ex-neotype culture CBS 134632 = LG4; MBT175922).

*Ectostromatic discs* circular, oblong or elliptic, 1–5.2 mm long, at times coalescent in small groups, typically surrounded by ruptured periderm, projecting up to 1 mm above the host surface, flat or convex, black, smooth or roughened. *Ostioles* opening separately in the disc, mostly umbilicate and inconspicuous, or papillate, sometimes strongly projecting above the disc surface, bluntly rounded to narrowly conical 0.2–0.9 mm high, 0.3–0.5 mm diam at the base, fragile. *Stromata* immersed in bark or erumpent, rarely superficial, particularly after the bark has split off, scattered or crowded; pustulate, bluntly conical or subglobose, 1.7–3.3(–12) mm diam, surrounded by a black stromatic



line, the latter 40–250 µm thick, irregular in outline, reaching down to the wood surface and spreading over it between adjacent stromata or surrounding several coalescent stromata. Tissue between ostiolar necks white or pale brown, tissue around and beneath perithecia typically light coloured, whitish to pale brown, composed of bark tissue mixed with white fungal tissue in variable proportions, at times bark hardly altered. *Perithecia* arranged in valsoid configuration, mostly 2–25, rarely to c. 100 per stroma, monostichous in smaller stromata, polystichous in larger ones, subglobose or flask-shaped, 0.4–1 mm diam, somewhat laterally compressed when crowded, with short to long ostiolar necks converging toward the disc. *Asci* cylindrical, spore part (78–)88–110(–119) × (6.0–)6.5–8.0(–8.7) µm (n = 25), containing 8 uniseriate ascospores; apical ring thin, amyloid, (1.5–)1.8–2.2(–2.3) µm wide, (0.5–)0.7–1.1(–1.3) µm high (n = 26). *Ascospores* (8.8–)10.5–12.8(–14.5) × (3.7–)4.5–5.5(–6.0) µm, l/w = (1.6–)2.0–2.7(–3.3) (n = 106), oblong or narrowly ellipsoid, laterally compressed, becoming distorted and collapsing on the narrow side in lactic acid and broad side unchanged or broader than in KOH, smooth, with two guttules particularly when young; germ slit in 3 % KOH distinct but thin, mostly on the narrow side, circumferential.

**Cultures** — Colony radius at room temperature on MEA 15–17 mm after 35 d (22–26 mm after 2 mo, centrally inoculated plate not entirely covered after 4.5 mo); colony circular to slightly irregular, surface becoming covered by a thick and dense white mat of aerial hyphae, at times developing (greyish) brown spots or pustules, particularly in the colony centre, reverse whitish to yellowish, becoming greyish brown to black from the centre, odour indistinct; no asexual morph formed within 6 mo. Growth on PDA similar, colony dull whitish to light brownish, becoming zonate; no asexual morph detected.

**Distribution & Habitat** — Europe, in corticated, rarely decorticated branches of *Ulmus* spp., common; frequently found also on other hosts such as *Acer*, *Carpinus* or *Prunus*.

**Other specimens examined.** AUSTRIA, Burgenland, Bad Sauerbrunn, Hirmer Wald, grid square 8264/1, on branch of *Carpinus betulus*, 13 July 2004, W. Jaklitsch; Niederösterreich, Gießhübl, on branch of *Carpinus betulus*, 18 Mar. 2012, H. Voglmayr (WU 32051; culture LG20); Großsenzersdorf, Lobau, grid square 7865/1, on branch of *Ulmus minor*, 27 Feb. 2000, W. Jaklitsch; Hagenbrunn, Bisamberg-east side, grid square 7664/3, on branch of *Carpinus betulus*, 30 Oct. 1999, W. Jaklitsch; Vienna, 13th district, Schönbrunn-Gloriette, grid square 7863/2, on branch of *Acer campestre*, 26 Feb. 2003, W. Jaklitsch W.J. 2063 (WU 32102); 19th district, Himmelstraße, on branch of *Carpinus betulus*, 4 Apr. 2010, W. Jaklitsch (WU 32044; culture LG1); *ibid.*, on branch of *Ulmus glabra*, 24 Apr. 2010, W. Jaklitsch (WU 32045; culture CBS 133210 = LG2); 22nd district, Lobau, near Panozalacke, grid square 7865/1, on branch of *Ulmus minor*, 4 May 1996, W. Jaklitsch W.J. 852 (WU 32101); *ibid.*, on *Ulmus minor*, 9 Mar. 2002, W. Jaklitsch W.J. 1858 (W); *ibid.*, on *Ulmus minor*, 30 Apr. 2003, W. Jaklitsch W.J. 2108 (W); *ibid.*, on branch of *Prunus padus*, 18 Mar. 2012, W. Jaklitsch (WU 32050; culture LG18); *ibid.*, on *Ulmus minor*, 7 Apr. 2012, W. Jaklitsch (WU 32052; culture LG26); 23rd district, Maurer Wald, grid square 7863/1, on *Ulmus minor*, 7 Oct. 2000, W. Jaklitsch. — FRANCE, Ariège, Rimont, Las Muros, on branch of *Acer campestre*, 14 Mar. 2011, J. Fournier JF 11016 (WU 32048; culture LG6); *ibid.*, on branch of *Ulmus minor*, 9 Nov. 2011, J. Fournier JF 11166 (WU 32047; culture LG5); *ibid.*, on branch of *Acer campestre*, 12 Nov. 2011, J. Fournier JF 11170 (WU 32049; culture LG7). — GREECE, Corfu, Liapades, on branch of *Ulmus minor*, 20 Apr. 2012, W. Jaklitsch (WU 32053); Skripero, shortly before the village heading north, on branch of *Ulmus minor*, 23 Apr. 2012, W. Jaklitsch & H. Voglmayr (WU 32054); Agia Anna, on branches of *Ulmus minor*, 23 Apr. 2012, W. Jaklitsch (WU 32055). — POLAND, Pulawy-Kepa, on *Ulmus* sp., 17 Nov. 1963, J. Kochman (NY; Mycotheca Polonica, fasc. XIV, no. 343). — SPAIN, Cataluña, Val d'Aran, Puerto de Bonaigua, elev. c. 2 000 m, on branch of *Sorbus chamaemespilus*, 16 May 1986, F. Candoussau (WU 32092).

**Notes** — The main arguments for how to define and circumscribe *L. gastrinum* are the plurivorous character and its primary occurrence on *Ulmus*, as already noted by Fries (1823), who mentioned *Ulmus* as the first host. No type material has been found at C, S and UPS. According to S. Ryman (pers. comm.),

there is a specimen in UPS, which bears the text '*Sphaeria gastrina*, junior? Lund' on the label, written by Elias Fries, i.e. Fries was apparently not sure of the determination of this specimen. The material is not sent out.

*Lopadostoma gastrinum* is common on *Ulmus* spp., occurs also on various other hardwood trees, but has not been detected on species of *Fagus* and *Quercus*. Stromata of this species are very variable, sometimes distinctly projecting or even superficial, which made a morphological delimitation of other species difficult in the pre-molecular era. Stroma development and ostioles are much dependent on climate conditions, particularly repeated drying and wetting in nature. Typical of *L. gastrinum* is its light, often nearly white entostroma in all parts, which is similar to that of *L. lechatii*. However, the latter species seems to be confined to *Carpinus* and has distinctly smaller ascospores. Ascospores of *L. gastrinum* are distinctly laterally compressed unlike those of other species of the genus. However, it is difficult to separate measurements of wide and narrow sides, therefore the whole range of ascospore widths is given above. No asexual morph has been detected in *L. gastrinum* on MEA and PDA.

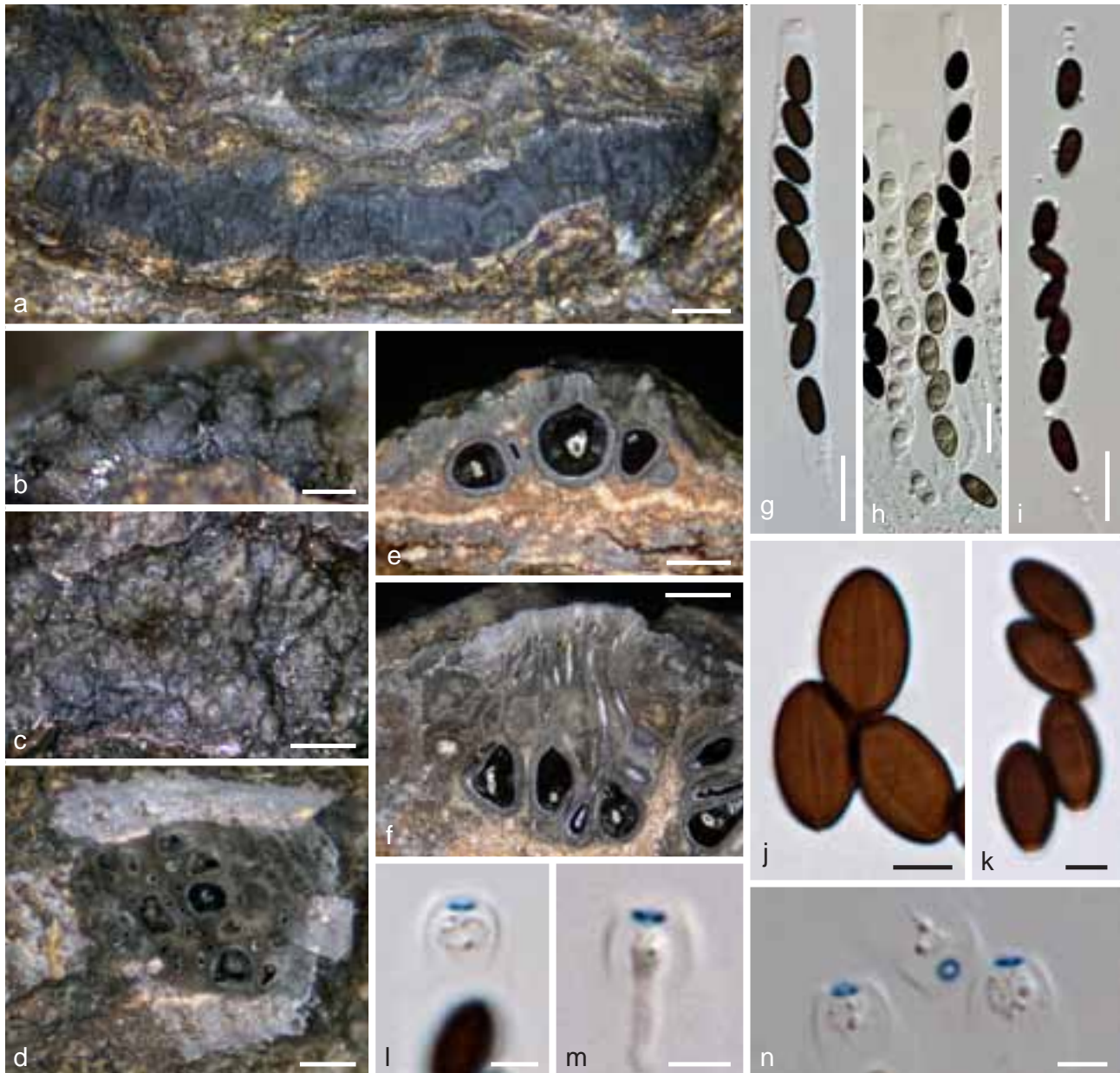
The combination *Phaeosperma gastrinum* (Fr.) Nitschke ex G.H. Otth, Mitth. Naturf. Ges. Bern: 42 (1869) [1868] was not published by Otth, but is based on an error made by Saccardo. Only *P. dryophilum* was published by Otth in the cited paper.

***Lopadostoma insulare*** Jaklitsch, J. Fourn. & Voglmayr, *sp. nov.*  
— MycoBank MB803806; Fig. 9

**Holotype.** SPAIN, Islas Baleares, Mallorca, Es Capdella, between Camí del Graner del Delme and Torrent de Galatzó, on a branch of *Quercus ilex* lying in wet grass, 16 Nov. 2010, W. Jaklitsch (WU 32056; ex-type culture CBS 133214 = LQM).

**Etymology.** Occurring on islands.

**Ecotromatic discs** usually ill-defined, massive, rounded or more or less ellipsoid, 0.7–4.8 mm diam, often coalescent into linear rows or irregular aggregates 9–16 mm long, projecting 0.4–2 mm above the host surface, flat or convex, tubercular or verrucose, black. *Ostioles* opening separately in disc, variable, umbilicate in the disc or papillate and bluntly rounded, or conical and projecting to 0.8 mm above the disc surface, 0.3–0.5 mm diam at the base, 0.1–0.3 mm diam at the apex, fragile. *Stromata* subglobose pulvinate or more or less effused, 2.3–10 mm diam, immersed in bark tissue, widely and irregularly erumpent; superficial on wood upon bark disintegration, laterally delimited by a thin, often inconspicuous black carbonized stromatic line, the latter irregular in outline, extending down to the wood surface and spreading over it between adjacent stromata. Tissue between ostiolar necks conspicuously dark greyish brown to blackish, woody, turning lighter to pale brown around and beneath the perithecia, composed of bark tissue mixed with white fungal tissue. *Perithecia* 3–80 per stroma, arranged in valsoid configuration, often densely crowded, monostichous in smaller stromata, polystichous in larger ones, subglobose or flask-shaped, 0.4–1.2 mm diam, often laterally compressed, with short to long ostiolar necks converging toward disc. *Asci* cylindrical, long-stipitate, spore part (53–)60–72(–79) × (4.5–)5.5–7.0(–7.5) µm (n = 36), with 8 uniseriate ascospores, sometimes oblique or biseriolate in the middle; apical apparatus c. 4.5 µm high and wide, containing a flat ring, refractive in KOH, dark blue in Lugol, (1.5–)1.6–1.8(–2.0) µm wide, (0.4–)0.5–0.7(–0.8) µm high (n = 30). *Ascospores* narrowly ellipsoid or oblong, not or indistinctly compressed, (6.2–)7.2–9.2(–11.0) × (3.0–)3.5–4.0(–4.7) µm, l/w = (1.7–)1.9–2.5(–3.1) (n = 85), chocolate to blackish brown, smooth, with circumferential, straight, germ slit, with 2 guttules when young, without dwarf cell, sometimes a narrow sheath on 1 side visible in asci.



**Fig. 9** *Lopadostoma insulare*. a–c. Ectostromatic discs (b. showing projecting ostioles); d. transverse stroma section; e, f. vertical stroma sections; g–i. asci (i. in Lugol); j, k. ascospores showing germ slit (j. compressed, showing slit on both sides); l–n. apical ascus rings in Lugol (a, e, g, h, j, n: LG32; b–d, f, i, k–m: LQM). — Scale bars: a, d, e = 0.7 mm; b = 0.5 mm; c, f = 1 mm; g–i = 10  $\mu$ m; j–n = 3  $\mu$ m.

**Cultures** — Colony radius at room temperature on MEA 27–30 mm after 35 d, centrally inoculated plate nearly entirely covered after 4.5 mo; colony circular, flat, surface covered by a thin mat of aerial hyphae, radial at the margin, white, slowly turning pale rosy, indistinctly zonate, slightly farinose; reverse yellowish to rosy, odour unpleasant; no asexual morph formed within 5 mo. On PDA colony similar to MEA, but more zonate, growth slightly more slowly.

**Distribution & Habitat** — Southern Europe, only known from two specimens collected in the islands Corfu and Mallorca on *Quercus coccifera* and *Q. ilex*.

**Other specimen examined.** GREECE, Corfu, Agia Anna, on corticated branch of *Quercus coccifera*, 23 Apr. 2012, H. Voglmayr & W. Jaklitsch (WU 32057; culture LG32).

**Notes** — The two known specimens of *L. insulare* differ considerably from each other. The distinctly projecting ostioles of the holotype specimen from Mallorca are apparently a consequence of the wet habitat on the ground, and its stromata may at first sight be identified as belonging to *Camarops* or *Valsaria*. The entostroma of this species is conspicuously dark.

Ascospores of *L. insulare* are amongst the smallest in *Lopadostoma* and help to distinguish this species from *L. meridionale*, which occurs on the same hosts and forms an asexual morph unlike *L. insulare*.

***Lopadostoma juglandinum*** (Rehm) Sacc. & Trotter, Syll. Fung. 22: 374. 1913. — Fig. 4f–s

≡ *Anthostoma juglandinum* Rehm, Ann. Mycol. 7: 531. 1909.

= *Anthostoma juglandinum* var. *caryae* Rehm, Ann. Mycol. 7: 531. 1909.

= *Lopadostoma juglandinum* var. *caryae* (Rehm) Sacc. & Trotter, Syll. Fung. (Abellini) 22: 375. 1913.

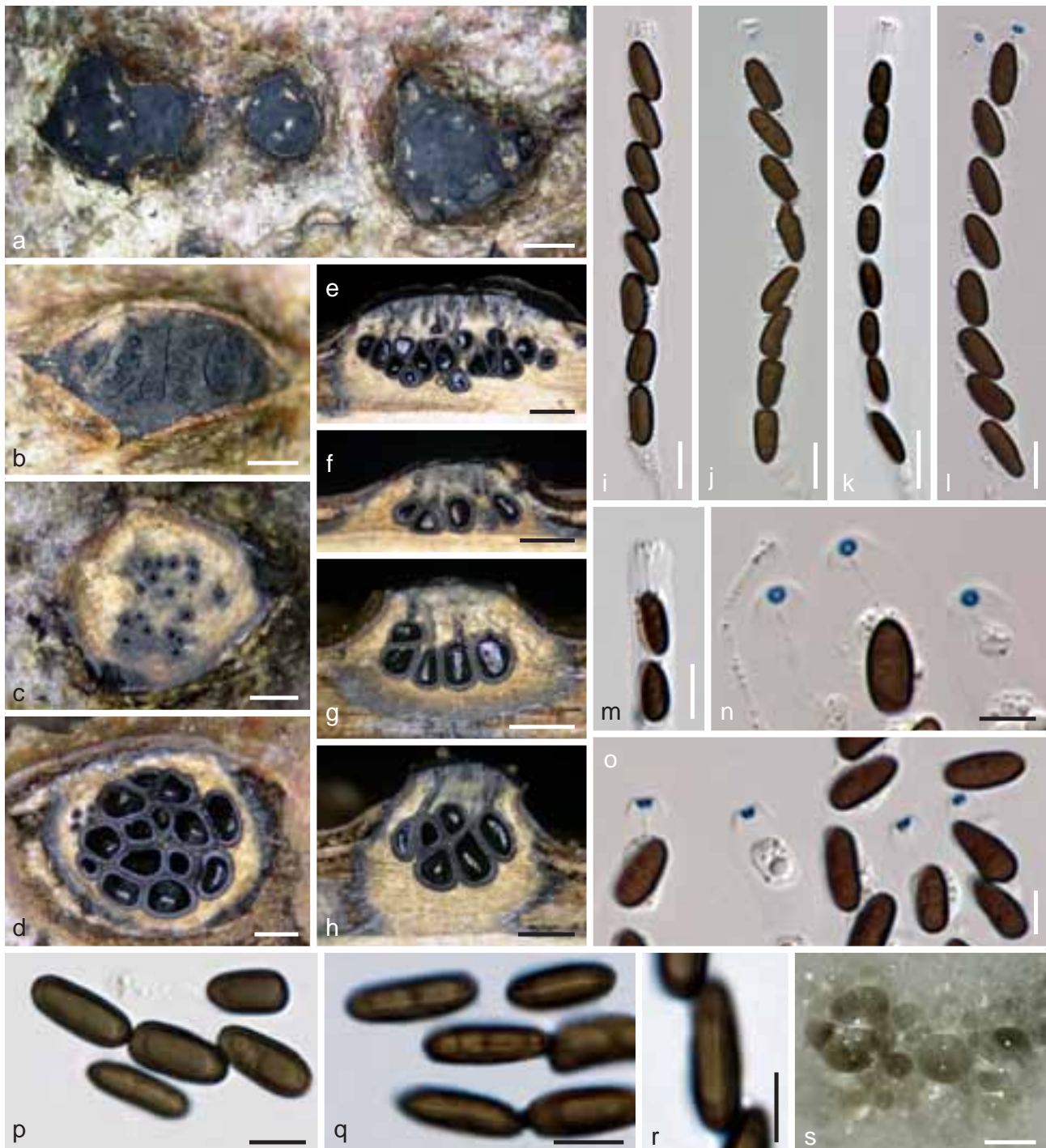
**Holotype of *Lopadostoma juglandinum*.** USA, Illinois, Port Byron, on hickory (*Carya alba*), 23 May 1904, E.T. & S.A. Harper No 1079 (C0004151F; as *Anthostoma juglandinum*, in F). Lectotype of *L. juglandinum* var. *caryae*, selected here: USA, Illinois, River Forest, on *Carya alba*, 20 Mar. 1909, E.T. & S.A. Harper (C0004152F; as *A. juglandinum* var. *caryae* No 2390 in F: MBT175916; isoelectotypes in M, NY and Kew (K(M) 177255)).

**Ectostromatic discs** extremely variable, either separate and more or less circular (0.3–)0.5–1.5 mm diam, or more commonly ill-defined, arranged in more or less linear rows to forming a con-



tinuum several (e.g. 4) cm long and up to 3 mm broad, often fused, cracked into smaller, ill-defined pieces without distinct separation, projecting from the bark surface to 0.5 mm (up to 1.7 mm in material named as var. *caryae*), dark brown, dark grey to black, sometimes pale brown, flat, convex or pulvinate, smooth or tubercular. *Ostioles* inconspicuous and umbilicate in the disc or shiny black and convex or sometimes discoid and grey, 100–200  $\mu\text{m}$  diam. *Stromata* densely arranged, erumpent from bark, extensive, widely effused, several cm long, containing several to many perithecial clusters and ostiolar discs, 0.8–3.5(–4) mm high, encased by a black line, the latter lacking between perithecial clusters within the stroma. *Entostroma* light-coloured, tissue between ostiolar necks whitish to pale greyish brown, darker brown in var. *caryae*, tissue

between and beneath perithecia pale brownish, whitish mottled, comprising white hyphae mixed with bark cells. *Perithecia* numerous, crowded, mostly monostichous, clustered in valsoid configuration, subglobose or flask-shaped, often laterally compressed, 0.4–0.9 mm high, 0.3–0.8 mm wide. *Ostiolar necks* 0.2–1 mm long, slightly converging upwards. *Asci* easily disintegrating in KOH mounts, cylindrical, spore part (49–)59–76(–86)  $\times$  (5.7–)6.0–7.5(–9.0)  $\mu\text{m}$  ( $n = 40$ ), containing 8 uniseriate, material named as often distinctly overlapping ascospores; apical apparatus short, semiglobose, 4.5–5.5  $\mu\text{m}$  wide, 2.5–3  $\mu\text{m}$  high, containing a refractive, amyloid, (1.6–)1.8–2.2(–2.3)  $\mu\text{m}$  wide and (0.4–)0.5–0.8(–1.0)  $\mu\text{m}$  high ( $n = 20$ ) apical ring in broadly rounded apex, often obscured by the uppermost ascospore. *Ascospores* oblong or ellipsoid, sometimes slightly



**Fig. 10** *Lopadostoma lechatii*. a, b. Ectostromata discs; c, d. transverse stroma sections (c. ostiolar level); e–h. vertical stroma sections; i–l. asci (l. in Lugol); m–o. apical ascospore rings (n, o. in Lugol); p–r. ascospores showing germ slit; s. clear drops on the colony centre on MEA at 25 °C after 64 d (a, b, d, e, g, h: JF06079; c, f, i–s: LG22). — Scale bars: a, e, g = 1 mm; b–d, s = 0.5 mm; f, h = 0.8 mm; i, j, l, m = 7  $\mu\text{m}$ ; k = 10  $\mu\text{m}$ ; n–r = 5  $\mu\text{m}$ .



allantoid, (7.8–)9.0–11.8(–14.5) × (3.5–)4.0–4.7(–5.5) µm, l/w = (1.7–)2.0–2.8(–3.9) (n = 134), not compressed, dark brown, smooth, without dwarf cell, germ slit distinct, commonly visible within asci, straight to slightly sinuous, circumferential.

Distribution & Habitat — North America (Illinois, Maine), in corticated branches of *Carya alba*.

*Other specimens examined.* USA, Illinois, Glencoe, on bark of *Carya alba*, 17 Apr. 1909, E.T. & S.A. Harper (K(M) 177254; as *A. juglandinum*); Maine, Kittery Point, on hickory (*Carya alba*), 1 Sept. 1930, R. Thaxter, det. L.E. Wehmeyer 6174 (M; as *A. juglandinum* var. *caryae*).

Notes — This species is currently only known from old herbarium specimens. Stromata of *L. juglandinum* are *L. gastrinum*-like regarding the pale-coloured entostromatic tissues, but differ by their sizes and wide expansion with many perithecial clusters, which are not encased by black lines. This latter feature recalls *L. quercicola*, but stromata of the latter species are much smaller and occur in species of *Quercus* in Europe. *Lopadostoma juglandinum* var. *caryae* is a more massive form of *L. juglandinum*, and although the stroma between ostiolar necks is sometimes darker in that variety, there are no statistical differences in microscopic data between the two varieties. Therefore recognition of a distinct variety may not be justified.

***Lopadostoma lechatii*** Jaklitsch, J. Fourn. & Voglmayr, sp. nov. — MycoBank MB803807; Fig. 10

*Holotype.* FRANCE, Poitou-Charentes, Deux Sèvres, Villiers en Bois, La Taillée, on corticated twig of *Carpinus betulus*, 11 Mar. 2012, C. Lechat CLL 12009 (WU 32058; ex-type culture CBS 133694 = LG22).

*Etymology.* Named in honour of the French collector and ascomycete connoisseur Christian Lechat.

*Ectostromatic discs* circular or elliptical in outline, black, often with flaps of periderm laterally adhering to it, 1–3.6 mm long, at times coalescent in small groups of 2–3, projecting up to 1.2 mm above the host surface, flat or slightly convex, smooth or roughened. *Ostioles* opening separately in the disc, umbilicate in the disc or slightly raised-discoid, typically inconspicuous. *Stromata* pustulate-erumpent from bark, scattered or densely crowded, rarely in contact, subglobose and 2.3–5.8 mm wide or pulvinate and 2–2.5 mm wide and 1–1.2 mm high, with flattened base, laterally delimited by a grey to black line; the latter 120–200 µm thick, irregular in outline, reaching to the wood surface and spreading over it between adjacent stromata or uniting several perithecial groups. Tissue between ostiolar necks whitish or yellowish, woody; tissue around and beneath perithecia yellowish to pale brown, composed of bark tissue mixed with white fungal tissue in variable proportions; bark often scarcely altered. *Perithecia* 12–25 per stroma, arranged in valsoid configuration, monostichous in smaller, polystichous in larger stromata, subglobose or flask-shaped, 0.4–0.8 mm diam, somewhat laterally compressed when crowded, with short to long ostiolar necks converging upward. *Asci* cylindrical, long-stipitate (stipe e.g. 45 µm long), spore part (63–)67–80(–85) × (5.0–)5.5–6.7(–7.5) µm (n = 30), with 8 uniseriate spores and flat apical ring (1.5–)1.6–2.0(–2.2) µm wide, (0.5–)0.8–1.1(–1.2) µm high (n = 31), refractive in KOH, dark blue in Lugol. *Ascospores* variable in shape, ellipsoid, oblong, cylindrical, angular, sometimes inequilateral, (7.5–)8.0–9.5(–11.0) × (3.0–)3.5–4.3(–4.5) µm, l/w = (1.8–)1.9–2.6(–3.3) (n = 30), blackish brown, greyish brown when young, smooth, slightly laterally compressed, with narrow sheath in asci, straight, circumferential germ slit on narrower side visible in water, becoming invisible in KOH and in Lugol.

Cultures — Colony radius at room temperature on MEA 6–9 mm after 35 d, 11–13 mm after 2 mo; growth rate enhanced by 1 % peptone; colony circular to irregularly lobate, becoming several mm thick in the colony centre, indistinctly zonate,

margin thin, hyaline; surface white to pale brown; after 2 mo colony centre with black spots or pustules and clear, colourless, grey-olive or black drops to 1 mm diam, not containing conidia; reverse yellowish to dull pale to dull grey-brown (5CD3–5). Chlamydospores common, globose or subglobose, (4.5–)5.0–9.0(–11.5) µm diam (n = 30), thick-walled. Odour strong, unpleasant, varnish-like. Growth and colony on PDA similar to MEA.

Distribution & Habitat — Only known from Western France on *Carpinus betulus*.

*Other selected specimens examined.* FRANCE, Charente Maritime, La Villedieu, Forêt d'Aulnay, on corticated branch of *Carpinus betulus*, 28 Apr. 2006, J. Fournier JF 06077 (WU 32090); Deux Sèvres, Forêt de Chizé, carrefour de l'Empereur, on corticated branch of *Carpinus betulus*, 24 Apr. 2006, J. Fournier JF 06079 (WU 32089).

Notes — This species is well defined by its small, often angular ascospores and the slowest growth of all species recognised here. Ascospore size is similar to that of *L. insulare*, which occurs on species of *Quercus* on Mediterranean islands and has a dark entostroma. The whitish entostromatic tissue of *L. lechatii* recalls *L. gastrinum*, which has distinctly larger ascospores and faster growth. *Lopadostoma lechatii* is common on its host in the region, where the above collections were made.

***Lopadostoma linoasperum*** (Durieu & Mont.) Jaklitsch, J. Fourn. & Voglmayr, comb. nov. — MycoBank MB803808; Fig. 11

*Basionym.* *Sphaeria linoasperma* Durieu & Mont. in Durieu de Maisonneuve, Expl. Sci. Algerie 1: 467. 1846.

= *Diatrype linoasperma* (Durieu & Mont.) Mont., Syll. Gen. Sp. Crypt.: 217. 1856.

= *Anthostoma linoasperum* (Durieu & Mont.) Sacc., Syll. Fung. 1: 305. 1882.

*Typification.* The type folder of *Sphaeria linoasperma* Durieu & Mont. in PC consists of three specimens, with the following information: ALGERIA, in bark of *Pistacia lentiscus*, C. Montagne: Durieu (Mostaganem, in cortice Lentisci), without collection dates; PC0085766 (= MC8671; MBT175917), the best preserved specimen is here selected as the lectotype of *Sphaeria linoasperma*. PC0085764 (= MC8670) and PC0085765 (= MC8669 = MS4242599) are isoelectotypes. Epitype here designated: ITALY, Sardinia, Oliena, near the hotel Su Gologone, on branch of *Pistacia lentiscus*, 3 Nov. 2009, W. Jaklitsch (WU 32059; MBT175918; ex-epitype culture CBS 133208 = LPL).

*Ectostromatic discs* circular, oblong or elliptical in outline, 0.7–2.7 mm in their greatest dimension, brown or blackish, projecting up to 1.2 mm above the host surface, flat, convex or pulvinate, shiny in places. *Ostioles* opening separately in the disc, umbilicate, inconspicuous, less commonly distinct, convex to papillate, black, shiny, 100–300 µm diam. *Stromata* pustulate, immersed to slightly erumpent, scattered, separate or coalescent in groups of 2–5, subglobose, 2–4 mm diam, surrounded by a black stromatic line; the latter irregular in outline, reaching the wood surface and spreading over it between adjacent stromata. Tissue between the ostiolar necks olivaceous yellow, prosenchymatous, abundant and conspicuous, not yielding a pigment in 10 % KOH, soft-textured, extending downwards between the perithecia, turning whitish and progressively merging with the basal tissue which is composed of slightly bleached bark tissue. *Perithecia* 4–20 per stroma, in valsoid configuration, monostichous in smaller stromata, polystichous in larger ones, ovoid to obpyriform, often laterally compressed, 0.7–1 mm high, 0.5–0.85 mm wide, with long ostiolar necks converging toward the disc. *Asci* cylindrical, containing (4–)8 uniseriate, partly overlapping ascospores, spore-bearing part (96–)107–127(–145) × (6.3–)6.8–8.5(–9.5) µm (n = 45); apical ring flat, refractive, amyloid, (1.6–)2.0–2.4(–2.6) µm wide, (0.5–)0.6–1.1(–1.2) µm high (n = 33). *Ascospores* oblong to nearly



**Fig. 11** *Lopadostoma lino-spermum*. a–o. Sexual morph: a. panoramic view of ostiolar discs; b, c. ectostromatic discs; d. transverse stroma section; e, f. vertical stroma sections; g–j. asci (g. in Lugol); k–n. apical ring and ascospores (m, n. in Lugol); o. ascospore showing germ slit. — p–v. Cultures and asexual morph on PDA at 22–25 °C: p. colony (55 d); q. conidial drop (62 d); r–v. conidia (63 d) (a, d–f, h–j, l, m, o: LPL; c: lectotype PC0085766; g, k, n, p–v: LPL1). — Scale bars: a = 2.5 mm; b–f, q = 0.5 mm; g–j, s = 15 µm; k, l = 7 µm; m = 5 µm; n, o = 3 µm; p = 10 mm; r, t–v = 10 µm.



cylindrical, (12.2–)13.5–17.3(–20.3) × (4.0–)5.0–6.2(–7.5) μm, l/w (2.0–)2.4–3.2(–4.0) (n = 112), often longest in basal position, not or slightly compressed, unicellular, blackish brown, smooth, with a straight, circumferential, spore-length germ slit.

Cultures and asexual morph — Ascospores germinating on MEA after 4–5 d; colony radius at room temperature on MEA 15–20 mm after 35 d; colony circular, surface covered by a cottony white mat of aerial hyphae, margin turning brown, brown pigment diffusing into the agar, reverse pale yellowish to brownish. Conidia forming after 1.5 mo in the colony centre

in 1–1.6 mm long, subhyaline, dull yellowish to pale brownish, mucous conidial pustules on 1–3 μm wide, smooth or warted conidiophores. Conidia (16–)20–25(–27) × (1.3–)1.4–1.6(–1.8) μm, l/w (10.8–)12.5–17.4(–19.1) (n = 30), hyaline, falcate, 1-celled, smooth, strongly curved to semicircular, with a long, nearly straight, narrowly truncate end and a short, strongly curved, acute end. Colony on PDA as on MEA, but darker and whitish/brownish zonate, conidia forming in colourless to pale yellowish drops in the colony centre.



**Fig. 12** *Lopadostoma meridionale*. a–p. Sexual morph: a, b. panoramic view of ectostromatic discs; c. ectostromatic discs; d, e. transverse stroma sections (d. ostiolar level); f, g. vertical stroma sections; h–k. asci (j, k. in Lugol); l–n. apical rings (m, n. in Lugol); o, p. ascospores showing germ slit. — q–u. Asexual morph on MEA at 25 °C after 48 d: q, r. conidial drops; s–u. conidia (a, c, d, h, j, l, m, o. LG29; b, e–g. LG10; i, k, n, p–u. LG). — Scale bars: a, b = 1 mm; c, d = 0.4 mm; e–g = 0.7 mm; h–k, s = 10 μm; l–p, u = 5 μm; q, r = 0.5 mm; t = 7 μm.

Distribution & Habitat — Europe and North Africa, on corticated branches of *Pistacia lentiscus* in the Mediterranean region.

*Other specimens examined.* SPAIN, Andalucía, Alcalá de los Gazules, Santuario de Nuestra Señora de los Santos, N36°26'58", W5°46'16.5", on branch of *Pistacia lentiscus*, 17 Mar. 2011, W. Jaklitsch & H. Voglmayr (WU 32061; culture LPL2); Andalucía, road A2226 to Benalup, at km 10, on branches of *Pistacia lentiscus*, 18 Mar. 2011, W. Jaklitsch (WU 32060; culture LPL1). Without geographic data, no collection date, on bark of *Pistacia lentiscus*, D.S. Corell, ex herb. M.J. Berkeley (K(M) 177258).

Notes — *Lopadostoma linospermum* is the counterpart of *L. dryophilum* on *Pistacia lentiscus*, based on ascospore characteristics and the yellow-olivaceous interostiolar stromatic tissue. However, apart from the different host it also forms an asexual morph in contrast to *L. dryophilum*. At first sight stromata of *L. linospermum* often resemble those of a *Diatrypella*.

***Lopadostoma meridionale*** Jaklitsch, J. Fourn. & Voglmayr, sp. nov. — MycoBank MB803809; Fig. 12

*Holotype.* CROATIA, Istria, Barbariga, forest N of the village, elev. c. 20 m, on a branch of *Quercus ilex*, 24 Sept. 2010, W. Jaklitsch (WU 32062; ex-type culture CBS 133209 = LG).

*Etymology.* *Meridionale* means southern; owing to its primarily southern distribution in Europe.

*Ectostromatic discs* circular or ellipsoid, 0.7–2.3 mm in their greatest dimension, projecting 0.3–0.7 mm above the often darkened, grey or brown host surface, pulvinate, convex or flat, often irregularly roughened or tubercular, shiny in places. *Ostioles* opening separately in the disc, umbilicate, inconspicuous. *Stromata* pustulate, scattered, separate or coalescent in groups of 2–6, subglobose, 1.8–4 mm diam, immersed in bark tissue, erumpent, surrounded by a black carbonised stromatic line 80–120 µm thick, irregular in outline, usually constricted beneath the stroma, reaching the wood surface and spreading over it between adjacent stromata. Tissue between ostiolar necks black, woody, not extending downwards between the perithecia, the tissue below the perithecia dull brownish with whitish spots, composed of slightly bleached bark tissue and whitish hyphae. *Perithecia* 3–10 per stroma, arranged in valsoid configuration, monostichous in smaller stromata, polystichous in larger ones, ovoid, obpyriform or flask-shaped, often laterally compressed, 0.8–1 mm high and 0.7–1.2 mm wide, with long ostiolar necks converging toward the disc. *Asci* cylindrical, spore part (68–)74–95(–113) × (6.2–)6.5–7.5(–8.5) µm (n = 60), containing 8 uniseriate ascospores, stipe c. 50 µm long; apex thickened, with a flat subapical, refractive, amyloid ring (1.8–)1.9–2.2(–2.4) µm wide, (0.5–)0.7–1.0(–1.2) µm high (n = 40). *Ascospores* oblong or narrowly ellipsoid, sometimes reniform or banana-shaped, (8.7–)10.3–12.8(–14.8) × (3.5–)4.0–4.8(–5.5) µm, l/w = (1.6–)2.3–3.1(–3.8) (n = 135), not distinctly compressed, first hyaline, turning yellow-brown and eventually dark brown, smooth, with 1–2(–3) guttules and inconspicuous, narrow, straight, circumferential germ slit, with thin sheath on one side in the ascus, dwarf cell lacking.

Cultures and asexual morph — Growth highly variable among strains (n = 7) but also within a single isolate, colony radius at room temperature on MEA 15–30 mm after 35 d, sometimes growth stopping after reaching a colony radius of 10–15 mm, remaining yellowish or turning brownish. Colony circular, thin or surface covered with a thick, cottony, white, radially structured mat of aerial hyphae or tufts along the margin, first white, turning yellowish or brownish, sometimes with a faintly rosy tint, sometimes zonate; reverse yellowish or dull yellow, turning brown in the centre, sometimes developing brown to black spots, accompanied by the formation of a diffusing reddish brown pigment. Odour either unpleasant and 'chemical' or more

or less fruity. After 1.5 mo conidia forming in mucous, yellow to orange, brown to black drops or pustules. Conidia falcate, (19–)22–27(–30) × (1.2–)1.3–1.5(–1.7) µm, l/w = (11.9–)14.8–20.1(–22.5) (n = 30), hyaline, 1-celled, strongly curved to nearly circular, with truncate base and acute end, smooth. On PDA growth sometimes distinctly faster than on MEA and colony covering a 90 mm Petri dish in 4.5 mo at room temperature, sometimes colony distinctly yellow.

Distribution & Habitat — Europe, on corticated branches of *Quercus coccifera* and *Q. ilex*; widely distributed, particularly in the Mediterranean region.

*Other specimens examined.* CROATIA, Istria, Rovinj, holm oak wood NW Monsena, on a branch of *Quercus ilex*, 17 May 2012, H. Voglmayr (WU 32068; culture LG36); Ugljan, northern tip of the island, on branch of *Quercus ilex*, 8 Aug. 1996, W. Jaklitsch W.J. 906 (WU 32103). — FRANCE, Ardèche, Vallon Pont d'Arc, banks of the river Ardèche, on branch of *Quercus ilex*, 2 May 2012, J. Fournier JF 12070 (WU 32069; culture LG40); Charente Maritime, Ile de Ré, Saint Martin en Ré, on a branch of *Quercus ilex*, 26 Apr. 2006, J. Fournier JF 06087 (WU 32063; culture LG10). — GREECE, Corfu, Agia Anna, on branch of *Quercus coccifera*, 23 Apr. 2012, H. Voglmayr & W. Jaklitsch (WU 32065; culture LG33); Kanakades, on branch of *Quercus ilex*, 20 Apr. 2012, H. Voglmayr & W. Jaklitsch (WU 32064; culture LG29); Prinilas, shortly after Vistonas above Prinilas, on branch of *Quercus coccifera*, 23 Apr. 2012, H. Voglmayr & W. Jaklitsch (WU 32066; culture LG34); Prinilas, white road to the left before entering Prinilas, on branch of *Quercus ilex*, 23 Apr. 2012, W. Jaklitsch & H. Voglmayr (WU 32067; culture LG35).

Notes — Morphologically, *L. meridionale* is characterised by rather small, irregular ectostromatic discs, well-developed dark brown to black tissue between the ostiolar necks and intermediate ascospore size between *L. insulare* and *L. dryophilum*. *Lopadostoma quercicola* has similar ascospores, but occurs on different species of *Quercus*. *Lopadostoma meridionale* is so far the only species of the genus on *Quercus* in Europe that yielded an asexual morph on MEA. However, the asexual morph has not been seen in all strains. The data given by Ju et al. (1993; as *L. turgidum*) for the asexual morph obtained with an isolate from French material on *Quercus ilex* suggest that they studied *L. meridionale*.

In some isolates early termination of growth was observed, which seems to be correlated with the formation of a diffusing pigment and strong unpleasant odour and therefore might be a consequence of self-intoxication. Such results were more pronounced in strains of *L. quercicola*.

***Lopadostoma quercicola*** Jaklitsch, J. Fourn. & Voglmayr, sp. nov. — MycoBank MB803810; Fig. 13

*Holotype.* AUSTRIA, Niederösterreich, Pfaffstätten, on *Quercus pubescens*, 15 Apr. 2012, H. Voglmayr (WU 32079; ex-type culture CBS 134633 = LG27).

*Etymology.* Occurring on *Quercus*.

*Ectostromatic discs* separate or clustered in small groups of 2–3 or more or in more or less long rows at the bottom of cracks in thick bark, grey or black, usually not surrounded by ruptured periderm, circular or elliptical in outline, 0.4–2 mm in their greatest dimension, flush with the surface or distinctly convex-pulvinate, projecting up to 0.8 mm above the bark surface, smooth to roughened. *Ostioles* opening separately in the disc, inconspicuous and umbilicate or more commonly distinct, flat and shiny or rounded-papillate, 70–240 µm wide, rarely distinctly projecting and stout. *Stromata* pustulate, often pulvinate and widely erumpent, often gregarious, usually containing several perithecial groups; the latter subglobose, usually not delimited by a black stromatic line, the latter only present around the entire stroma and running between bark and wood. Tissue between ostiolar necks brown, dark grey to blackish, woody, extending downwards between perithecia; tissue around and beneath perithecia composed of hardly altered, slightly





**Fig. 13** *Lopadostoma quercicola*. a, b. Stroma surface; c–e. ectostromatic discs; f–h. transverse stroma sections (f. ostiolar level); i–k. vertical stroma sections; l–o. asci; p–r. apical ascus rings (q, r. in Lugol); s–u. ascospores showing germ slit (u. compressed, showing slit on both sides) (a, k: LG17; b, d, l, m, r, u: LG12; c, h, j, o, t: LG27; e, f, i, q, s: LG3; g, n: LG25; p: LG38). — Scale bars: a = 2 mm; b = 1.5 mm; c–e = 0.3 mm; f–k = 0.6 mm; l–p = 10 µm; q, u = 7 µm; r–t = 5 µm.

bleached bark tissue and whitish spots of fungal mycelium. *Perithecia* 4–16 per stroma, arranged in valsoid configuration, usually monostichous, rarely polystichous in larger groups, subglobose or flask-shaped, 0.4–1 mm diam, somewhat laterally compressed when crowded, with short to long ostiolar necks converging toward the disc. *Asci* cylindrical with stipes to c. 50 µm long, spore part (66–)72–91(–108) × (4.3–)5.8–7.3(–8.5) µm (n = 60), containing 8 more or less uniseriate, often overlapping ascospores and a refractive, amyloid, (1.5–)1.8–2.0(–2.2) µm wide and (0.5–)0.6–0.8(–1.0) µm high (n = 33) ring in a subglobose apical apparatus. *Ascospores* oblong or narrowly

ellipsoid, (8.7–)9.5–12.0(–14.3) × (3.8–)4.3–5.0(–5.5) µm, l/w = (1.8–)2.1–2.7(–3.2) (n = 140), longest in basal position, not compressed, first hyaline, then smoky grey-brown, with 1–2 large guttules, eventually dark, chocolate to blackish brown, smooth, with a narrow hyaline perispore 0.5 µm thick visible on one side in asci, with a straight or slightly sinuous, circumferential germ slit.

Cultures — Colony radius at room temperature on MEA 11–19 mm after 35 d, 22–28 mm after 2 mo. Colony circular, thin and smooth, sometimes with radial folds, surface and reverse (pale) yellow, e.g. 4A3–4, sometimes with a rosy tint, aerial

hyphae scant or lacking; odour unpleasant, strong, varnish-like, also when colony yellow and no diffusing pigment is formed. No asexual morph formed on MEA within 6 mo. Colony sometimes remaining small with a radius of 10–13(–17) mm, turning grey or greyish brown, reverse turning brown to black and brown pigment diffusing in the agar. Growth and colony on PDA similar to MEA.

**Distribution & Habitat** — Europe, in corticated branches of *Quercus cerris*, *Q. petraea*, *Q. pubescens* and *Q. suber*, possibly also *Q. robur*; widely distributed, particularly common around Vienna, Austria.

*Other specimens examined (all on corticated branches)*. AUSTRIA, Niederösterreich, Gießhübl, on *Quercus petraea*, 18 Mar. 2012, *H. Voglmayr* (WU 32077; culture LG19); Heiligenkreuz, close to the highway exit, on *Quercus cerris*, 16 Mar. 2012, *H. Voglmayr* & *W. Jaklitsch* (WU 32075; culture LG16); *ibid.*, on *Quercus petraea*, 16 Mar. 2012, *H. Voglmayr* & *W. Jaklitsch* (WU 32076; culture LG17); Siegenfeld, shortly after the village heading to Gaaden, on a corticated branch of *Quercus cerris*, 16 Mar. 2012, *W. Jaklitsch* & *H. Voglmayr* (WU 32072; culture CBS 133212 = LG12); *ibid.*, on *Quercus petraea*, 16 Mar. 2012, *H. Voglmayr* & *W. Jaklitsch* (WU 32073; culture LG14); *ibid.*, on *Quercus cerris*, 16 Mar. 2012, *H. Voglmayr* & *W. Jaklitsch* (WU 32074; culture LG15); Waxeneck, NE Pernitz, near Schutzhaus, on *Quercus petraea*, 9 June 2013, *H. Voglmayr* & *I. Greilhuber* (LI); Vienna, 19th district, Hermannskogel, grid square 7763/2, on branch of *Quercus cerris*, 11 Feb. 1995, *W. Jaklitsch* W.J. 489 (WU 32104); *ibid.*, on *Quercus cerris*, 19 Aug. 1995, *W. Jaklitsch* W.J. 710 (WU 32105); *ibid.*, on *Quercus cerris*, 27 Mar. 1999, *W. Jaklitsch* W.J. 1294 (WU 32107); Vogelsangberg, on *Quercus cerris*, 3 Mar. 2012, *W. Jaklitsch* & *H. Voglmayr* (WU 32071; culture LG9); 23rd district, Maurer Wald, grid square 7863/1, on *Quercus cerris*, 19 Oct. 1996, *W. Jaklitsch* W.J. 987 (WU 32106). — CROATIA, Istrija, Rovinj, at the road Rovinj-Bale, c. 2 km W Bale, on *Quercus cerris*, 18 May 2012, *H. Voglmayr* (WU 32080; culture LG37); Rovinj, field edge N of the nature preserve Palud, on *Quercus pubescens*, 19 May 2012, *H. Voglmayr* (WU 32081; culture LG38); Vižinada, NW Žudetići, at the road to Ponte Porton, on *Quercus cerris*, 20 May 2012, *H. Voglmayr* (WU 32082; culture LG39). — FRANCE, Côte d'Or, forêt de Longchamp, near Maison Forestière du Tertre, elev. 240 m, on *Quercus* sp. (*Q. petraea* or *Q. robur*), 13 Oct. 2005, *P. Leroy* PL05414D; Indre et Loire, Bois de Roche-Monts, on *Quercus* sp. (*Q. petraea* or *Q. robur*), 30 May 2006, *P. Leroy* PL06222C (WU 32078; culture LG25); Loir et Cher, Boulogne, carrefour du roi de Pologne, on *Quercus* sp. (*Q. petraea* or *Q. robur*), 22 Oct. 2004, *P. Leroy* PL04435A. — ITALY, Sardinia, Aggius, on branch of *Quercus suber*, 7 Nov. 2009, *W. Jaklitsch* (WU 32070; culture LG3). — PORTUGAL, Oeiras, on branch of *Quercus suber*, Nov. 1978, *A.M. Macava* (WU 32094).

**Notes** — *Lopadostoma quercicola* is one of the five species recognised here on *Quercus*. Stromata of this species are often widely erumpent and contain many perithecial groups, similar to *L. juglandinum*. The black stromatic line is often invisible, because it only surrounds the whole stroma, not the individual perithecial groups within the stroma. *Lopadostoma americanum* differs from *L. quercicola* by its occurrence on white oaks in North America, ill-defined ectostromatic discs, slightly wider ascospores, faster growth and formation of an asexual morph; *L. insulare* by distinctly smaller ascospores and occurrence on the evergreen oaks *Quercus coccifera* and *Q. ilex* on Mediterranean islands; *L. meridionale* by occurrence on the evergreen oaks *Quercus coccifera* and *Q. ilex* and formation of an asexual morph; and *L. dryophilum* differs by larger ascospores and a yellow-olivaceous entostroma between the ostioles.

Frequently slow and early terminated growth of several strains is correlated with a discolouration of the colony to grey-brown and black on the reverse and by diffusion of a grey- to dark brown pigment into the agar. Such cultures can often be revived by transfer to fresh medium. The strong, varnish-like odour is also formed when the colony is yellow and fast-growing and no diffusing pigment is formed. In *L. meridionale* the diffusing pigment occurs less commonly and is more reddish brown.

***Lopadostoma turgidum* (Pers.) Traverso, Fl. Ital. Crypt. 1, 1, 2: 170. 1906. — Fig. 14**

**Typification.** From the two original specimens of Persoon present in L, L0108269 and L0108272 (no collection data given), L0108272 (MBT175919) is here selected as lectotype of *Sphaeria turgida*. Epitype here designated: AUSTRIA, Niederösterreich, Gaaden, 3 Dec. 2011, *H. Voglmayr* (WU 32085; ex-epitype culture CBS 133207 = LT2; MBT175920).

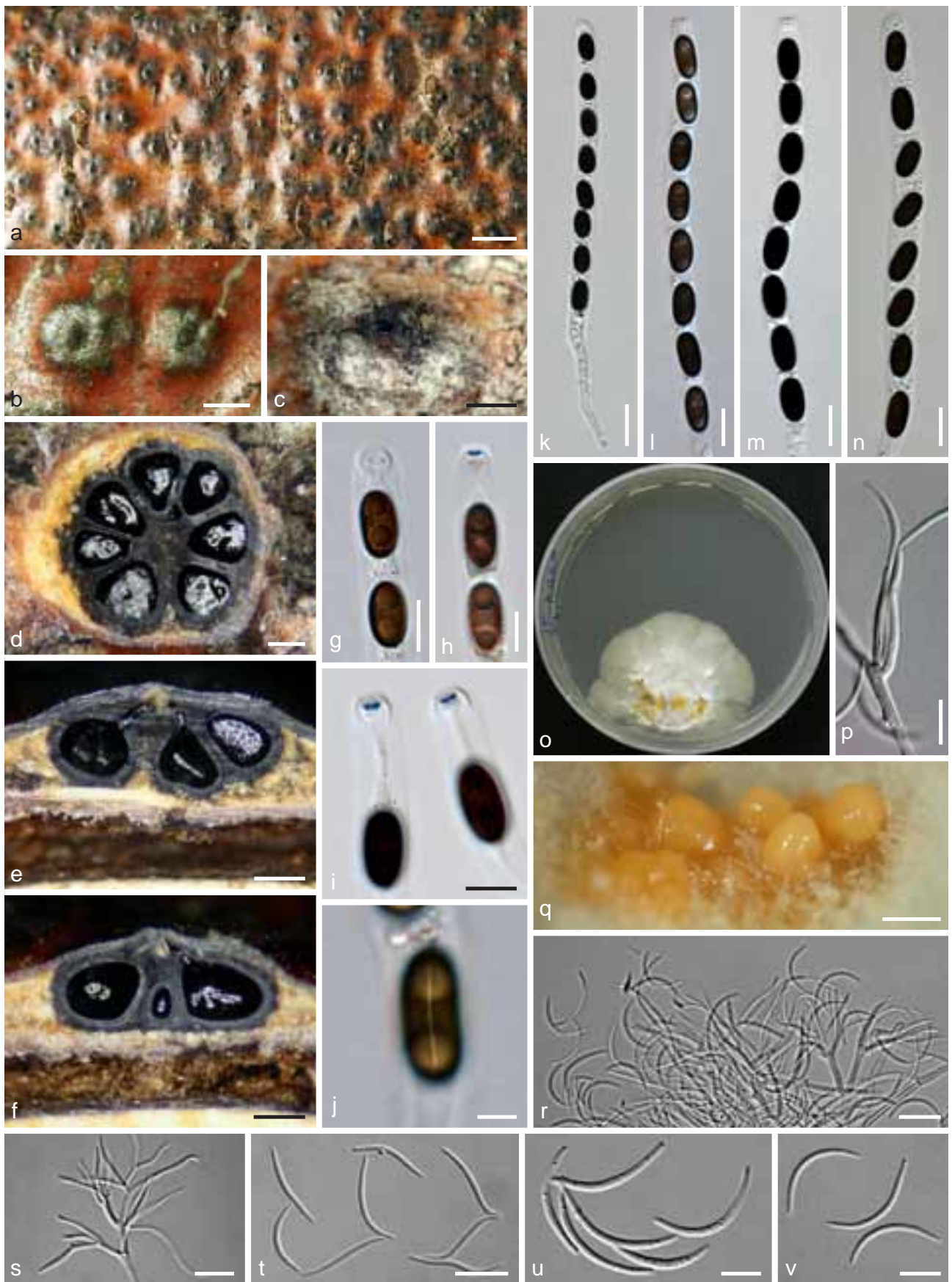
**Basionym.** *Sphaeria turgida* Pers., *Observ. Mycol. (Lipsiae)* 1: 17. 1796. = *Anthostoma turgidum* (Pers.) Nitschke, *Pyrenomyces Germanici* 1: 121. 1867.

**Stromata** widely effused on recently dead branches, up to 30–40 cm long, uniting numerous small, typically densely gregarious, separate or coalescent, flattened pustules 1–2 mm diam, slightly raising the periderm and discolouring it dark silvery grey above the pustules, contrasting with the surrounding reddish brown colour; perithecial mounds at the pustule margin often distinct. Centre of pustules pierced by a dark grey to black ectostromatic disc (0.20–)0.25–0.45(–0.55) mm diam (av. = 0.3 mm, n = 110), circular or elliptic in outline, flat, slightly convex or concave, flush with the bark surface or more rarely projecting 40–170 µm above it, surrounded by teeth-like remnants of the ruptured bark. The tissue between the ostioles and above the perithecia blackish, soft-textured, the tissue surrounding perithecia somewhat powdery, composed of white fungal tissue mixed with yellowish brown bark cells; the tissue beneath perithecia more solid, composed of hardly decayed host tissue delimited in the lower part by a thin, often inconspicuous dark brown to black stromatic line; loosening bark below stromata seated on a thick dark brown feltly layer spreading over the wood surface. *Perithecia* 3–8(–10) per stroma, monostichous, circinate, densely aggregated, subglobose to depressed-globose, (0.45–)0.5–0.7(–1.1) mm diam, with long ostiolar necks converging toward the disc, opening separately in the disc. *Ostioles* umbilicate, inconspicuous or invisible. *Asci* cylindrical, long stipitate (e.g. stipe 55 µm long), containing 8 uniseriate ascospores, spore-bearing part (72–)94–112(–119) × (6.5–)7.0–8.3(–8.7) µm (n = 51), amyloid ring (2.0–)2.2–2.5(–2.7) µm wide, (0.3–)0.5–0.8(–0.9) µm high (n = 15). *Ascospores* ellipsoid, (8.5–)10.2–12.2(–13.7) × (5.0–)5.5–6.0(–6.5) µm, l/w (1.5–)1.7–2.1(–2.5) (n = 94), dark brown to nearly black, opaque when mature, smooth, with straight spore-length germ slit on one side only, and 2 large guttules when young; lowest ascospore in the ascus often longer than others.

**Cultures and asexual morph** — Ascospores germinating on MEA after 2–3 d; colony radius at room temperature on MEA 17–18 mm after 35 d, 35–37 mm after 4.5 mo. Colony circular with well-defined margin, white, turning brown from the centre; reverse turning dark brown with orange-brown margin, yellow-brown pigment diffusing into the agar; odour indistinct. Cream, pale yellow to orange mucous masses of conidia forming after 1.5–2 mo in effuse spots or well-defined pycnidia c. 1 mm diam. Conidiophores simple, formed in white floccules on a wide moniliform, thick-walled stipe to 9.5 µm wide, asymmetrically branched in narrow angles into verticils of terminal branches 1–3.5 µm wide, bearing long cylindrical to subulate, straight or curved phialides singly or in whorls of 2–6. Conidia falcate, (15–)20–26(–31) × (1.3–)1.5–1.7(–1.9) µm, l/w (8.8–)12.2–17.4(–20.3) (n = 63), hyaline, 1-celled, smooth, upper end nearly acute, base truncate, slightly to distinctly curved, with minute guttules. On PDA similar to MEA, but lighter coloured, brownish with hyaline or white margin; conidia forming in orange-brown drops.

**Distribution & Habitat** — Europe, in corticated branches of *Fagus sylvatica*; common.





**Fig. 14** *Lopadostoma turgidum*. a–n. Sexual morph: a. panoramic view of stromata; b. two stromata in face view; c. ectostromatic disc; d. transverse stroma section; e, f. vertical stroma sections; g–i. apical ring and ascospores (h, i. in Lugol); j. ascospore showing germ slit; k–n. asci. — o–v. Cultures and asexual morph: o. colony with asexual morph; p, r, s. conidiophores (p. showing phialide bearing conidium); q. pycnidia; t–v. conidia (o–v: all on MEA at 25 °C after 70–74 d. a, c–f: LT; b, j, k, n, o, q, u: LT2; g–i, l, m, p, r–t, v: LT1). — Scale bars: a = 1.5 mm; b = 0.7 mm; c–f = 0.3 mm; g–i, u = 7 µm; j = 3 µm; k, r–t = 15 µm; l–n, p, v = 10 µm; q = 1 mm.

*Additional specimens and records*, all from corticated branches of *Fagus sylvatica*. AUSTRIA, Kärnten, St. Margareten im Rosental, Stariwald, elev. 600 m, grid square 9452/4, 27 Dec. 1994, *W. Jaklitsch* W.J. 402 (WU 32108); *ibid.*, 11 July 2011, *W. Jaklitsch* (WU 32083; culture LT); *ibid.*, Zabrede, 12 Aug. 1995, *W. Jaklitsch*; Rechberg, grid square 9453/3, 6 Sept. 1998, *W. Jaklitsch*; Niederösterreich, Hainbuch, grid square 7763/1, 28 Sept. 1996, *W. Jaklitsch*; Lahnsattel, virgin forest Neuwald, from Donaudörfel, grid square 8259/1, 31 July 1999, *W. Jaklitsch*; Lunz am See, Rothwald 2, grid square 8256/2, 3 July 1999, *W. Jaklitsch*; Mauerbach, 31 July 2011, *W. Jaklitsch* (WU 32084; culture LT1); Ottenstein, Dobra-Stausee: virgin forest at the dam, grid square 7458/1, 28 Sept. 2003, *W. Jaklitsch*; Steiermark, Berghausen, Graßnitzberg, grid square 9259/4, 20 Sept. 1996, *W. Jaklitsch*; Pöllau, Schönauklamm, grid square 8760/2, 12 Sept. 2002, *W. Jaklitsch*; Tirol, Tristach, Buchwiese, grid square 9142/4, 30 Aug. 2000, *W. Jaklitsch*; Vienna, 19th district, Kahlenberg, grid square 7763/2, 15 Dec. 1996, *W. Jaklitsch*; Cobenzl, grid square 7763/2, 5 July 1998, *W. Jaklitsch* W.J. 1172 (WU 32109); 23rd district, Maurer Wald, grid square 7863/1, 3 Oct. 1998, *W. Jaklitsch*. – FRANCE, Ariège, Prat-Communal, Loumet, elev. 900–950 m, 21 Apr. 2012, *J. Fournier* JF 12051; Rimont, Las Muros, Grand Bois, combe Fourcade, elev. 750 m, 9 Nov. 2011, *J. Fournier* JF 11165 (WU 32086; culture LT3); Hautes Pyrénées, Castillon, Moulin de Sarthe, elev. 360 m, 9 Apr. 2011, *J. Fournier* JF 11030. Numerous additional records from Austria, Czech Republic, Denmark, Germany, The Netherlands, United Kingdom, based on gross morphology, i.e. distinction from *L. fagi* uncertain.

**Notes** — *Lopadostoma turgidum* is common on *Fagus* in Europe, but is at times locally nearly entirely replaced by *L. fagi*, which differs in slightly larger ectostromatic discs (0.5 vs 0.3 mm in average), smaller ascospores, a circumferential germ slit and different culture characteristics like rosy colony reverse and faster growth. Stromata of both species differ from those of other species in that they are more valsoid than diatrypelloid, with little stromatic tissue present below the perithecia.

At first sight *L. turgidum* and *L. fagi* may be easily confounded with *Quaternaria quaternata*, which is extremely common on *Fagus* and often co-occurs with them. The latter can, however, be distinguished under a lens by its distinct ostioles that are not embedded in a compact disc.

A specimen from New York (Rensselaer Co., Taborville, Cherry Brook Recreation Area, 10 Sept. 1977, *M.E. Barr Bigelow* 6409 (NY)) on *Fagus grandifolia* has extremely small stromata with only the minute black discs visible, but otherwise unchanged bark surface. Ascospores, however, are in agreement with *L. turgidum*. Proof of conspecificity would require fresh material and gene sequences.

The lectotypification of *L. turgidum* by Lu & Hyde (2000) is invalid, because they selected material collected by C. Montagne, which was not part of Persoon's original material. They, however, correctly noted that *L. turgidum* is type of the genus, examined also the two original specimens of Persoon and gave a description, which matches our findings.

## EVALUATION OF TAXA IN LOPADOSTOMA, ANTHOSTOMA AND PHAEOSPERMA

Including infraspecific taxa, there are at least 183 combinations in *Anthostoma* (21 missing in Index Fungorum and MycoBank), 31 in *Lopadostoma* and 18 in *Phaeosperma*. Many names have been removed from these genera to others such as *Amphisphaerella*, *Anthostomella*, *Apiorhynchostoma*, *Barrmaelia*, *Biscogniauxia*, *Camarops*, *Capronia*, *Coniochaeta*, *Cryptosphaeria*, *Didymella*, *Dyrithium*, *Endoxyla*, *Entoleuca*, *Eutypa*, *Gigantospora*, *Helicogermis*, *Hypoxylon*, *Immotthia*, *Jumillera*, *Lepteutypa*, *Leptomassaria*, *Loculohypoxylon*, *Pseudovalsaria*, *Quaternaria*, *Rosellinia*, *Splanchnonema*, *Whalleya* and *Xylomelasma*.

All names in *Lopadostoma* and some names in *Anthostoma*, which are not treated above and initially thought to be relevant

in this context, are commented on below. Relevant names in *Phaeosperma* are included as synonyms of species treated under the accepted species above or in the commentary below.

### 1) Names in Lopadostoma

***Lopadostoma amoenum*** (Nitschke) Shear, *Mycologia* 30, 5: 593. 1938. — Fig. 15a–h

≡ *Fuckelia amoena* Nitschke, *Jahrb. Nassauischen Vereins Naturk.* 23–24: 224. 1870 (1869–1870).

= *Anthostoma amoenum* (Nitschke) Sacc., *Syll. Fung. (Abellini)* 1: 307. 1882.

A recent collection from France, Deux Sèvres, Villiers en Bois, Forêt de Chizé, Rimbaud, on dead twig of *Fagus sylvatica*, 14 Apr. 2008, *P. Leroy* (JF 08072; culture MUCL 51842 = LA; kindly provided by M. Stadler) was studied:

*Stromata* immersed in bark, scattered, pustulate, erumpent, 0.4–1 mm diam, appearing on the bark surface as small white to yellowish granular ectostromatic discs containing 1–5 convergent but separately opening ostioles; the latter 100–160 µm wide, smooth, black, rounded at the top, flush with the stromatal surface to slightly projecting. *Perithecia* arranged in valsoid configuration, subglobose with flattened base to lenticular, 0.4–0.5 mm wide, 0.2–0.3 mm high, surrounded by decayed cortical tissue; black stromatic line absent. *Ostiolar necks* central or more commonly eccentric and oblique. *Paraphyses* simple, abundant. *Asci* cylindrical, with 8 uniseriate ascospores, short-stipitate, 140–160 µm long, with a massive, diamond-shaped, 6.5–7.5 µm wide and 2.5–4 µm high, apparently bipartite, amyloid apical ring, with the lower part stronger bluing in iodine than the upper. *Ascospores* broadly ellipsoid with narrowly rounded ends to citriform, (18.5–)20.8–24.0(–25.7) × (10.2–)11.5–13.2(–14.7) µm, l/w = (1.5–)1.6–2.0(–2.5) (n = 34), 1-celled, equilateral, olive-brown, smooth, with a central to eccentric, rounded and 2.5–3 µm wide germ pore and bipolar cellular appendages 1 µm thick and 3 µm broad; contents with numerous large and small guttules.

**Notes** — This specimen is in agreement with the description of *Fuckelia amoena* by Læssøe & Spooner (1994) except for slightly smaller ascospores. Læssøe & Spooner (1994) studied two isotypes (K) and discussed similarities to and differences from *Lopadostoma* and *Euepixylon*. The latter shares the poroid germ locus with *L. amoenum*. Apart from morphology, also an LSU sequence obtained from the above specimen places the fungus outside *Lopadostoma*. The genus *Fuckelia* Nitschke is a later homonym of *Fuckelia* Bonord. 1864 and therefore unavailable.

***Lopadostoma apiculatum*** (Sacc.) P.M.D. Martin, *J. S. African Bot.* 42, 1: 75. 1976.

*Basionym.* *Sphaeria apiculata* Curr., *Trans. Linn. Soc. London* 22: 326. 1859 (non *Sphaeria apiculata* Wallr., *Fl. Crypt. Germ. (Norimbergae)* 2: 778. 1833).

= *Phaeosperma apiculatum* (Curr.) Sacc. & Traverso, *Syll. Fung.* 20: 326. 1911.

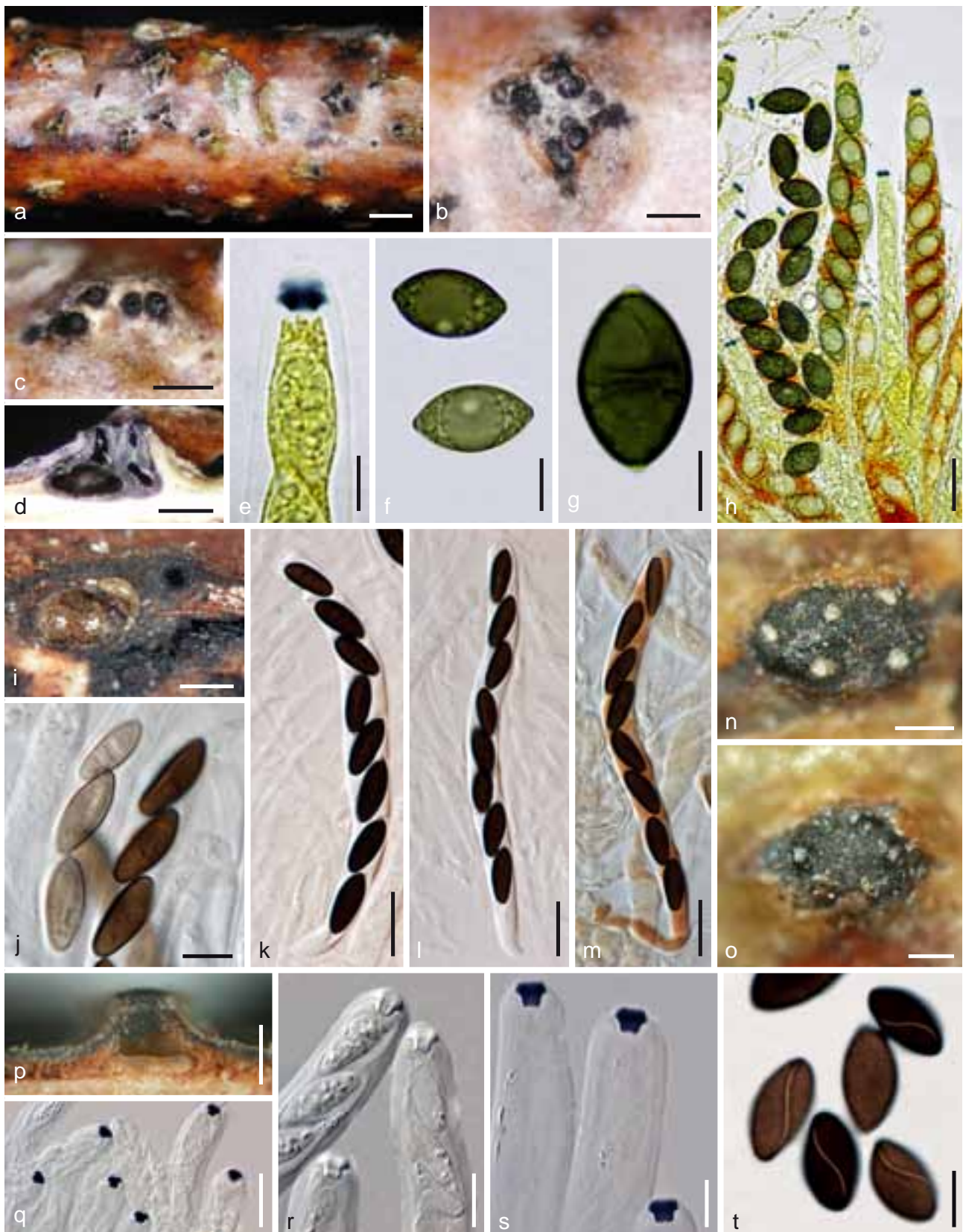
Current name — *Apiorhynchostoma curreyi* fide Petrak (1923; as *A. apiculata*) or Müller & von Arx (1962).

***Lopadostoma caespitosum*** (Ellis & Everh.) P.M.D. Martin, *J. S. African Bot.* 42, 1: 75. 1976.

*Basionym.* *Rosellinia caespitosa* Ellis & Everh., *Proc. Acad. Nat. Sci. Philadelphia* 46: 327. 1894.

This is a *Coniochaeta* sp. fide Barr et al. (1996).





**Fig. 15** a–h. '*Lopadostoma*' cf. *amoenum* (JF 08072). a. Habit; b, c. ectostromatic discs with ostioles; d. vertical stroma section; e. apical ascus ring in Lugol; f, g. ascospores; h. asci in Lugol. — i–m. *Anthostoma gastrinoides* (holotype K(M) 177256). i. Cut perithecium with gelatinous contents; j. ascospores; k–m. asci (m. in Lugol). — n–t. *Anthostoma insidiosum* (*Valsa insidiosa* holotype; CO). n, o. Ectostromatic discs with ostioles; p. vertical stroma section; q–s. apical ascus rings (q, s. in Lugol); t. ascospores. — Scale bars: a = 1 mm; b–d, i, p = 0.3 mm; e, g, j = 7  $\mu$ m; f, r, s = 10  $\mu$ m; h, q = 25  $\mu$ m; k–m, t = 15  $\mu$ m; n, o = 0.2 mm.

**Lopadostoma conorum** (Fuckel) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

*Basionym.* *Amphisphaeria conorum* Fuckel, Jahrb. Nassauischen Vereins Naturk. 29–30: 20. 1875 (1877).

= *Anthostoma conorum* (Fuckel) Cooke, Grevillea 17: 90. 1889.

Current name — *Anthostomella conorum* (Fuckel) Sacc. fide Francis (1975) and Lu & Hyde (2000).

**Lopadostoma cubiculare** (Fr.) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

*Basionym.* *Sphaeria cubicularis* Fr., Syst. Mycol. (Lundae) 2, 2: 477. 1823.

= *Anthostoma cubiculare* (Fr.) Nitschke, Pyrenomycetes Germanici 1: 113. 1867.

Current name — *Helicogermis* *fleischhakei* fide Læssøe & Spooner (1994) and Rappaz (1995).

**Lopadostoma dubium** (Feltgen) Sacc. & Trotter, Syll. Fung. 22: 375. 1913.

*Basionym.* *Anthostoma dubium* Feltgen, Vorstud. Pilzfl. Luxemb., Nachtr. II: 111. 1901.

Described from Luxembourg on *Corylus avellana* as forming valsoid perithecia and ascospores  $12\text{--}15 \times 4\text{--}6 \mu\text{m}$ . No material bearing this name was received from B, BR, K or LUX, therefore its identity remains unclear and doubtful.

**Lopadostoma flavoviride** (Ellis & Holw.) Rappaz, Mycol. helv. 7, 1: 129. 1995.

*Basionym.* *Anthostoma flavoviride* Ellis & Holw., in Arthur et al., Bull. Geol. Nat. Hist. Surv. 3: 32. 1887.

*Stromata* in wood, effuse. Not a species of *Lopadostoma* s.str., but belonging to *L.* subg. *Anthostomopsis*, which may eventually be split into several genera.

**Lopadostoma formosum** (Ellis & Everh.) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

*Basionym.* *Anthostoma formosum* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 46: 344. 1894.

The holotype, USA, Kansas, on dead limbs of *Celtis occidentalis*, 14 June 1894, *Bartholomew* No. 1492 (NY), was examined. The material is mostly depauperate, with partly disintegrated, black, convex or pulvinate discs  $0.4\text{--}1.6 \text{ mm}$  diam, with inconspicuous ostioles or irregular clusters of ostioles projecting up to 1 mm. *Stromatic tissue* within the black line is poorly developed and pale brownish. *Asci* cylindrical, spore part  $(72\text{--})75\text{--}88\text{--}(92) \times (6.0\text{--})6.3\text{--}7.3\text{--}(7.5) \mu\text{m}$  ( $n = 10$ ), containing 8 uniseriate ascospores and a flat refractive, amyloid ring. *Ascospores* oblong,  $(9.7\text{--})10.0\text{--}11.8\text{--}(14.8) \times (4.0\text{--})4.3\text{--}5.2\text{--}(5.5) \mu\text{m}$ , l/w  $(1.9\text{--})2.1\text{--}2.6\text{--}(3.0)$  ( $n = 30$ ), dark brown, light when young, smooth, without dwarf cell, germ slit along narrower side, circumferential, straight. Morphologically, *L. formosum* is thus in agreement with *L. gastrinum*, as indicated by Rappaz (1995) and on the label of the holotype.

**Lopadostoma gallicum** Sacc., Atti Mem. Accad. Sci. Lett. Arti, Padova 33: 159. 1917.

The holotype was examined in PAD: *Stromata* are immersed in bark of *Acer pseudoplatanus*, irregularly distributed or aggregated in lines. Internally they are white and surrounded by black lines. *Ostioles* slightly projecting and rounded or up to pentagonal in face view. The *stromata* are in accordance with those of *L. gastrinum*, but *asci* are long-stipitate, inamyloid and contain 8 ascospores in biseriate arrangement. *Ascospores*

are allantoid, dark brown, measure  $(7.0\text{--})7.8\text{--}10.5\text{--}(12.2) \times (2.5\text{--})2.7\text{--}3.3\text{--}(3.5) \mu\text{m}$ , l/w =  $(2.1\text{--})2.5\text{--}3.7\text{--}(4.2)$  ( $n = 35$ ) and lack a germ slit. Based on these traits *L. gallicum* is apparently a synonym of *Eutypella grandis* (Nitschke) Sacc.

**Lopadostoma hawaiianum** J.D. Rogers & Y.M. Ju, Canad. J. Bot. 80: 479. 2002.

Described from wood of *Casuarina*, Hawaii. A member of *Lopadostoma* subg. *Anthostomopsis*, i.e. not a species of *Lopadostoma* s.str.

**Lopadostoma helicoides** Lar.N. Vassiljeva, Novosti Sist. Nizsh. Rast. 27: 58. 1990.

On dead twigs of *Kalopanax septemlobus* in Primorye, Russia. Based on the protologue, this species does not belong to *Lopadostoma* because of the large ascospores ( $43\text{--}50 \times 14\text{--}17 \mu\text{m}$ ) having a spiralling germ slit.

**Lopadostoma helveticum** (Fuckel) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

*Basionym.* *Phaeosperma helvetica* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 224. 1870 (1869–1870).

Current name — *Camarops microspora* (P. Karst.) Shear (*Boliniaceae*), fide Nannfeldt (1972).

**Lopadostoma massarae** (De Not.) Traverso, Fl. Ital. Crypt. 1, 1, 1: 172. 1906.

*Basionym.* *Hypoxylon massarae* De Not., Sfer. Ital.: 17. 1863.

In corticated branches in Northern Italy, with a black stromatic line and dark disc; ascospores  $20 \times 8 \mu\text{m}$ . According to A. Graniti (pers. comm.) the species is indicated on the handwritten label of the sole specimen present in RO, as “*Sphaeria Massarae* DNtrs a Valtellina. Dr. Balsamo a Massara lecta 1836”. Unfortunately no response was obtained from RO, the name *Lopadostoma massarae* is therefore not interpretable. The only specimen present in PAD bearing this name consists of some pieces of bark of *Carpinus betulus*, with a polypore given as *Poria contigua* on the label and old, mostly disintegrated *stromata* of *Melogramma campylosporium*. No fungus matching the protologue could be found.

**Lopadostoma microecium** (Ellis & Everh.) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

*Basionym.* *Anthostoma microecium* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 46: 344. 1894.

This is *Coniochaeta* cf. *ligniaris* fide Rappaz (1995), based on the type.

**Lopadostoma microsporum** (P. Karst.) P.M.D. Martin, J. S. African Bot. 35: 400. 1969.

*Basionym.* *Anthostoma microsporum* P. Karst., Fungi Fenniae Exsicc., Fasc. 9: no. 860. 1869.

= *Phaeosperma microspora* (P. Karst.) P. Karst., Not. Sallsk. Fauna Fl. Fenn. Forh. 13: 240. 1873.

Current name — *Camarops microspora* (P. Karst.) Shear (*Boliniaceae*), fide Nannfeldt (1972).

**Lopadostoma ostropoides** (Rehm) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

Probably a *Helicogermis* sp. fide Læssøe & Spooner (1994).



***Lopadostoma polynesium*** (Berk. & M.A. Curtis) Rappaz, Mycol. Helv. 7, 1: 125. 1995.

*Basionym.* *Sphaeria polynesia* Berk. & M.A. Curtis, Grevillea 4, no. 32: 146. 1876.

A European specimen, which is morphologically in agreement with the description of *L. polynesium* by Rappaz (1995), was kindly provided by Alain Gardiennet: France, 21, Côte-d'Or, Savigny-le Sec, Combe Bonenfant, on *Amelanchier ovalis*, 5 May 2012, A. Gardiennet AG 12056 (WU 32088, culture LAG). This fungus superficially resembles the genus *Eutypa*, as perithecia are evenly immersed in a monostichous layer in light wood under a widely effused clypeus (blackened wood surface) and have long, non-clustered, vertically emerging, black ostioles. However, the ascospores are dark brown and narrowly ellipsoid to fusiform, not allantoid; they measure (8.5–)8.8–10.8(–12.0) × (3.5–)3.8–4.5(–4.8) µm, l/w = (1.8–)2.1–2.8(–3.4) (n = 30) and have an inconspicuous, narrow, straight, probably circumferential germ slit. They germinated very slowly (CMD) and only at low temperatures and the white, compact, c. 2 mm thick colonies with a peculiar brown (containing rosy and orange tones) reverse grew only at 15–20 °C on PDA, reaching a radius of c. 9 mm after 4.5 mo at 15 °C. LSU places this fungus outside *Lopadostoma* (Fig. 1). Yu-Ming Ju (pers. comm.) examined the holotype of *L. polynesium* and found that its ascospores contain a short germ slit, thus it is possible that the material from France is not the same species.

***Lopadostoma pouzarii*** Granmo & L.E. Petrini, Mycol. Helv. 8, 1: 44. 1996.

*Stromata* of this species differ from those of *Lopadostoma* in being effused, erumpent from decorticated wood (of *Fraxinus*, *Ulmus* and *Acer*), containing non-clustered perithecia with broadly ellipsoid ascospores and are therefore in accordance with *L.* subg. *Anthostomopsis*, as determined by the authors. Two cultures of this fungus, kindly provided by Marc Stadler, were sequenced and found not to belong to *Lopadostoma* (Fig. 1), but they also do not cluster with *L. cf. polynesium*. According to Yu-Ming Ju (pers. comm.), *L. pouzarii* belongs to another xylariaceous genus, probably *Whalleya* J.D. Rogers, Y.M. Ju & San Martín.

***Lopadostoma rhenanum*** (Fuckel) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

*Basionym.* *Fuckelia rhenana* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 224. 1870 (1869–1870).

Not a species of *Lopadostoma*. Described from Germany on *Acer pseudoplatanus*. Læssøe & Spooner (1994) studied two isotypes from K, which have (26–)32–37(–41) × 11.5–15(–17) µm large ascospores devoid of a germ locus.

***Lopadostoma saprophilum*** (Ellis & Everh.) Rappaz, Mycol. Helv. 7, 1: 129. 1995.

*Basionym.* *Anthostoma saprophilum* Ellis & Everh., J. Mycol. 3, 4: 43 (1887).

USA, N.J., Newfield, in wood of *Acer* sp. Included by Rappaz (1995) in his *L.* subg. *Anthostomopsis*, hardly distinguishable from *L. polynesium*. Not a member of *Lopadostoma*.

***Lopadostoma sphinctrinum*** (Kunze) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

*Basionym.* *Sphaeria sphinctrina* Kunze, in Kunze & Schmidt, Mykologische Hefte (Leipzig) 2: 48. 1823.

Described as having circinate perithecia on *Fagus sylvatica*. This may be a synonym of *L. turgidum*, but no type material is extant in B and TUB, therefore the name remains dubious.

***Lopadostoma stictoides*** (Ellis & Everh.) P.M.D. Martin, J. S. African Bot. 42, 1: 83. 1976.

*Basionym.* *Anthostoma stictoides* Ellis & Everh., nom. nud.

According to Martin (1976) stromata are immersed in wood of *Crataegus*, have white ostioles and brown ascospores 17.5 × 11 µm. This is based on the type, which was collected by Dearness in London, Ontario in 1892 and incorporated in the herbarium of Ellis in 1899 (NY). Læssøe & Spooner (1994) interpreted this fungus as a *Helicogermis* sp.; see also Barr et al. (1996).

***Lopadostoma taeniosporum*** (Sacc.) Traverso, Fl. Ital. Crypt., Pars 1: Fungi. Pyrenomycetae, Xylariaceae, Valsaceae, Ceratostomataceae 1, 1: 171. 1906.

*Basionym.* *Anthostoma taeniosporum* Sacc., Atti Soc. Veneto-Trentino Sci. Nat. Padova 2: 143. 1873.

Described from Italy in bark of *Quercus pedunculata* (a synonym of *Quercus robur*). The holotype (PAD) was briefly examined. *Perithecia* of this fungus are not obviously stromatic, but clustered in bark fissures. *Asci* are cylindrical, inamyloid and contain 8 uniseriate ascospores. *Ascospores* are broadly ellipsoid, (17.0–)17.5–20.5(–24.5) × (9.8–)10.7–12.7(–14.5) µm, l/w = 1.4–1.8(–2.5) (n = 35), unicellular, slightly laterally compressed, dark brown, equilateral, without sheath or appendages, and contain a unilateral, straight, spore-length germ slit. According to the protologue, stromata are first immersed in bark, become free and become disintegrated to liberate perithecia. The generic affiliation of *L. taeniosporum* is unclear, but the fungus clearly does not belong to *Lopadostoma*.

***Lopadostoma turgidum*** var. *minus* Sacc., Ann. Mycol. 6: 558. 1908.

Described from France, near Paris, on *Quercus* or *Castanea* with ascospores 8–9 × 4.5–5 µm. Doubtful, no material preserved in PAD.

***Lopadostoma turgisporum*** Lar. N. Vassiljeva, Pirenomits. Lokuloaskomits. Severa Dal'nego Vostoka (Leningrad): 200. 1987.

Described from *Betula ermanii* in Siberia, with ascospores 8–10 × 6–7 µm. This species may belong to *Lopadostoma*. It was not examined.

## 2) Some names in *Anthostoma*, which may be relevant in this context

***Anthostoma acerinum*** Ellis & Fairm., Proc. Rochester Acad. Sci. 4: 189. 1905.

This is a synonym of *Lopadostoma turgidum* fide Rappaz (1995), who identified the host as *Fagus* by xylotomy. This may be true if the species on *Fagus grandifolia*, which is microscopically in accordance with *L. turgidum*, is conspecific with the European species.

***Anthostoma adustum*** (Cooke & Peck) Sacc., Syll. Fung. 1: 307. 1882.

See under *Anthostoma insidiosum*.

***Anthostoma antarcticum*** Speg., Boln Acad. Nac. Cienc. Córdoba 11, 2: 195. 1888.

Described on *Nothofagus* (*Fagus betuloides*) from Tierra del Fuego with ascospores 8–13 × 3–3.5 µm. This may be a species of *Lopadostoma*, as far as interpretable from the protologue.

***Anthostoma decipiens*** (DC.) Nitschke, Pyrenomyces Germanici 1: 111. 1867.

*Basionym.* *Sphaeria decipiens* DC., in Lamarck & de Candolle, Fl. Franç., ed. 3 (Paris) 2: 285. 1805.

= *Lopadostoma decipiens* (DC.) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

= *Cryptosphaeria decipiens* (Lam. & DC.) Læssøe & Spooner, Kew Bull. 49, 1: 56. 1994 (1993).

The following specimen of *A. decipiens* was collected, cultured and sequenced in this work: AUSTRIA, Vienna, 19th district, Himmelstraße, on trunks of *Carpinus betulus*, 24. Mar. 2012, W. Jaklitsch (WU 32008; culture CBS 133221 = CD).

*Ascospores* germinate readily overnight on MEA; colony growing fast on this medium, white, yellowish to faintly rosy, odour indistinct; first conidia forming within 3 wk, in whitish patches, not in slimy drops. *Conidia* (9.0–)10.0–12.0(–13.5) × 1.5–1.8 µm, l/w = (5.3–)6.0–7.7(–9.0) (n = 33), allantoid, unicellular, hyaline, smooth, ends blunt.

LSU and ITS sequences are in accordance with GenBank accessions AM399021 and JN975370. The fungus does not belong to *Cryptosphaeria* or *Eutypella* and may form a genus of its own in the *Diatrypaceae*. This confirms the conclusions by Rappaz (1992). Currently only the type species *A. decipiens* is recognized in *Anthostoma*. So far, all other studied species of *Anthostoma* have been identified as belonging to other genera, but there are still many names to re-evaluate. Another candidate for *Anthostoma* may be *Eutypella phaeospora* (Fournier & Lechat 2011).

***Anthostoma gastrinoides*** (W. Phillips & Plowr.) Sacc., Syll. Fung. 1: 763. 1882. — Fig. 15i–m

*Basionym.* *Valsa gastrinoides* W. Phillips & Plowr., Grevillea 10: 71. 1881.

The holotype from England, Bristol, on twigs of *Viburnum* sp. (possibly *V. lantana*), Mar. 1880, Bucknall 6 (holotype K(M) 177256), was examined. The material consists of a *Diaporthe* sp. and small, depauperate, umbilicate discs with few papillate ostioles in bark; stromata c. 1.5–2.5 mm wide, immersed in the inner bark and upper wood layer, delimited by a black line (which may belong to the *Diaporthe*), lighter within the line, containing light-coloured circinate perithecia (e.g. 0.6 × 0.4 mm) with gelatinous contents. *Paraphyses* numerous, in a gelatinous matrix, richly branched. *Asci* 93–106 × 8–11.5 µm (n = 5), cylindrical, short-stipitate, with 4–8 overlapping uniseriate ascospores, thick-walled, with 1.5–2.5 µm thick, inamyloid apex, not containing a ring, disintegrating readily in mounts. *Ascospores* (13.0–)13.5–15.0(–16.5) × (5.0–)5.3–6.0(–6.5) µm, l/w = (2.2–)2.3–2.7(–2.9) (n = 21), oblong or narrowly ellipsoid, dark brown, with a diffuse, straight germ slit on one side, without dwarf cell, with a narrow sheath on one side in asci.

From this rather scant material it is not clear, whether the fungus is stromatic or perithecia are immersed in stromata of the *Diaporthe*. The microscopic features, particularly the inamyloid ascus apex and the ascospores point to *Anthostoma melanotes*, presently a synonym of *Barrmaelia oxyacanthae* (see Mathiasen (1993: 65), Rappaz (1995: 137) or Læssøe & Spooner (1994: 42) for descriptions). However, the gelatinous matrix swelling in water and containing richly branched hamathecial elements and the thick-walled inamyloid ascus apex may alternatively suggest a loculoascomycete.

***Anthostoma insidiosum*** (P. Crouan & H. Crouan) Sacc., Syll. Fung. 1: 306. 1882. — Fig. 15n–t

*Basionym.* *Valsa insidiosum* P. Crouan & H. Crouan, Florule Finistère: 32. 1867.

= *Diatrype adusta* Cooke & Peck, Ann. Rep. N.Y. State Mus. Nat. Hist. 29: 58. 1878 (1877).

= *Anthostoma adustum* (Cooke & Peck) Sacc., Syll. Fung. (Abellini) 1: 307. 1882.

= *Anthostomella adusta* (Cooke & Peck) M.E. Barr, in Barr et al., Bull. New York State Mus. 459: 6. 1986.

*Stromata* erumpent from bark, bluntly conical, small, 0.3–0.7 mm high, comprising a soft, whitish to brownish hyphal entostroma mixed with bark cells within a black line widely effused between bark and wood, rising above stromata and forming clypei or ectostromatic discs above 1–5 circinate perithecia with rather light-coloured walls; discs (0.6–)0.7–1(–1.2) mm wide, mostly convex, circular, oblong or often angular or irregular due to surrounding bark flaps, sometimes with few black shiny, flat or convex ostiolar dots 130–200 µm diam in the disc, some ostioles white and 60–90 µm wide, of highly variable length. *Paraphyses* numerous, narrow. *Asci* cylindrical, short-stipitate, with 8 uniseriate ascospores and a massive, plug-like, amyloid apical ring, dark blue to black in Lugol, 6.5–7.5 µm wide, 4.5–5.5 µm high. *Ascospores* (24–)25.5–29(–31.5) × (11.5–)12.5–15.5(–17) µm, l/w = (1.6–)1.8–2.1(–2.3) (n = 31), unicellular, (inequilaterally) ellipsoid to nearly citriform, dark brown, partly with thin hyaline sheath in the ascus, with sinuous to helical germ slit spore-length, without dwarf cell.

*Specimen examined.* FRANCE, Finistère, on bark of *Fagus sylvatica*, 6 June 1868, Crouan (holotype; CO), kindly provided by J.P. Priou.

Notes — Morphological characters including ascospore and ascus plug morphology are in agreement with *Anthostomella (Diatrype) adusta*; see also Læssøe & Spooner (1994: 44), Rappaz (1995: 148) and Barr et al. (1986: 6) for descriptions of *A. adusta*. Læssøe & Spooner (1994) noted that this fungus more likely represents a new genus, while Lu & Hyde (2000) suggested *Lopadostoma* sp. *Valsa insidiosa* (1867) predates *Diatrype adusta* (1878) and is therefore the valid epithet for this taxon. *Anthostoma insidiosum* does not belong to *Lopadostoma* despite its stromata, which resemble those of *L. gastrinum*, but are much smaller. Particularly the spiral germ slit in broadly ellipsoid ascospores and the massive apical ascal plug exclude this fungus from *Lopadostoma*.

***Anthostoma phaeospermum*** (Ellis) Sacc., Syll. Fung. II: XIV. 1883.

*Basionym.* *Diatrype phaeosperma* Ellis, Amer. Naturalist 1883: 195. 1883.

An examination of the holotype (USA, Iowa, branches of *Amelanchier canadensis*; NY) confirmed that this fungus belongs to *Diatrype*.

***Anthostoma plowrightii*** (Niessl) Sacc., Syll. Fung. I: 305. 1882.

*Basionym.* *Fuckelia plowrightii* Niessl, Hedwigia 14: 130. 1875.

On *Ulex* in England; ascospores given as 10–14 × 6–7 µm. No type material is extant in B, K and M.

***Anthostoma tetrastagum*** Delacr., Bull. Soc. Mycol. France 13: 124, t. 10, f. G. 1897.

In bark of *Quercus*, France. The protologue and original drawing, which show perithecia evenly immersed in bark and seated on brown mycelium and oblong, straight or curved, brown ascospores 18 × 6 µm, containing 4 guttules may suggest *Enchinoa infernalis*. No material was received from PC and MPU.

## DISCUSSION

Most genera of the *Xylariaceae* form true stromata, which are by definition entirely composed of fungal tissue. Others, such as *Anthostomella*, *Euepixylon*, *Helicogermisli*, *Leptomassaria*



or *Lopadostoma* form pseudostromata, which contain a mixture of fungal and host tissue. We studied one of the latter genera, *Lopadostoma*, which contained only few species, until Martin (1969, 1976) combined names of many unrelated fungi into this genus, and before Rappaz (1995) added his subgenus *Anthostomopsis*.

Delimitation of genera in the *Xylariales* and *Xylariaceae* has been based on morphology, asexual morphs and more recently also secondary metabolites (Læssøe & Spooner 1994, Ju & Rogers 1996, 1999, Bitzer et al. 2008), while DNA data have played a secondary role. A considerable number of nuclear DNA sequences of the ribosomal cluster are available in GenBank, but because of low variation in combination with homoplasy and thus low power of resolution (LSU), or poor alignability due to high length variability (ITS), sound phylogenetic and evolutionary inferences using markers like LSU and/or ITS are limited.

However, a phylogenetic analysis based on LSU (Fig. 1) was sufficient to make clear that *Lopadostoma*, which we reduce here to species with pustular stroma development in bark of broad-leaved trees and shrubs, forms a monophylum within the *Xylariaceae*, while *Lopadostoma* subg. *Anthostomopsis*, represented by the two species *L. cf. polynesium* and *L. pouzarii* do not belong to the genus. It is currently, however, not possible to establish a generic name for *L.* subg. *Anthostomopsis*, because the two species included do not fall into the same clade, i.e. this 'subgenus' is phylogenetically heterogeneous. More freshly collected material is needed to draw a clear picture of this assemblage of species. It appears also that the few accessions labelled with the generic name *Anthostomella* do not cluster together, i.e. this genus seems to be highly polyphyletic.

Sequences of protein-coding genes such as *act*, *tub* and *rpb2* have been shown to be superior to the ribosomal cluster in genera closely related to *Hypoxyylon* (Hsieh et al. 2005) and in *Xylaria* (Hsieh et al. 2010), but they are only available for few taxa of *Xylariaceae*. We used *rpb2* in combination with ITS and LSU to study species delimitation in *Lopadostoma* in detail (Fig. 2). Clustering of intraspecific isolates using this marker correlated well with morphology and hosts, except for *L. meridionale*, which is split into several well-supported subclades, despite uniformity of specimens and hosts. In *L. meridionale*, high genetic variability of these markers is present even within a small geographic area (see phylogenetic positions of LG29, LG33, LG34 and LG35, all sampled in northern Corfu, Greece, or LG and LG36 sampled in south-western Istria, Croatia). The significance of this result is not clear, we therefore leave the subclades of the *L. meridionale* clade taxonomically unresolved for the time being. In addition, morphological similarities among species are not reflected by the *rpb2*/ITS/LSU tree topology; for instance, *L. linspermum* and *L. dryophilum*, which share distinctly yellow-brown to olivaceous entostroma between ostiolar necks and large asci and ascospores are not closely related (Fig. 2).

Many species of *Lopadostoma* are morphologically difficult to distinguish, because of overlap of many features and considerable intraspecific variation, in part caused by changes of climatic factors during stroma development and maturation. Furthermore, sizes of *L. gastrinum*-like stromata (most species) are correlated with the diameter of the twig or branch on which they occur, i.e. with bark thickness and accordingly substrate availability. Thus qualitative characters like the colour of stromatic tissue between ostiolar necks or presence or absence of a black stromatic line around individual perithecial clusters, are more informative than quantitative ones (diameter of stromata, number of perithecia and their size), i.e. most morphological characters are too variable to be discriminant. More important is the combination of ascospore size, stroma colour between

ostioles and hosts. *Lopadostoma* encompasses mostly host-specific species, but *L. gastrinum* is plurivorous, with marked abundance on *Ulmus* spp. To a lesser extent, also other species may occur on different, but closely related hosts. As an exception, *L. fagi* was once found on *Corylus*, which is not closely related to its typical host. Slight differences of this strain from *Fagus*-isolates might eventually indicate a good species on a very fine-tuned scale. Species on *Quercus* may occur on different host species, which usually fall into different subgenera of *Quercus*. The diversity of *Lopadostoma* on the latter genus is by far the highest. Thus it is expected that regions with a high diversity of *Quercus* spp., such as North America and Mexico, may be home to additional undescribed species of *Lopadostoma*. So far, we have only seen one report of a *Lopadostoma* sp. (as *L. turgidum*) by San Martín & Lavin (1997) from *Quercus* sp. in Mexico with small ascospores ( $8-9.5(-11) \times 3.5-4 \mu\text{m}$ ).

Such concentration of bark-inhabiting species on a certain host genus is conspicuous, as other genera of similar ecology, e.g. *Massaria* and *Prosthecium* (*Stegonsporium*) on *Acer* (Voglmayr & Jaklitsch 2008, 2011) and *Melanconiella* on *Carpinus* and the closely related genus *Ostrya* (Voglmayr et al. 2012) behave similarly.

Based on current collections, the spatial distribution of *Lopadostoma* as circumscribed here appears to be restricted to temperate and Mediterranean Europe and to a lesser extent to North America. Remarkably, no confirmed records are known to us from East Asia, despite the widespread presence of suitable host genera like *Ulmus*, *Fagus* and *Quercus*, which may indicate that this region is largely understudied.

Species of *Lopadostoma* are generally not particularly common, but show a marked seasonal occurrence. Like many other pyrenomycetes they occur throughout Europe mostly in spring (March to May with a peak in April) and in autumn (September to November). During these periods they may be abundant in regions, where the respective hosts are common. Some species, particularly those on *Fagus*, viz. *L. fagi* and *L. turgidum*, may be also common in summer, depending on moisture.

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## REFERENCES

- Arx JA von, Müller E. 1954. Die Gattungen der amerosporen Pyrenomyceten. Beiträge zur Kryptogamenflora der Schweiz 11: 1–434.
- Barr ME, Huhndorf SM, Rogerson CT. 1996. The Pyrenomycetes described by J.B. Ellis. *Memoirs of the New York Botanical Garden* 79: 1–137.
- Barr ME, Rogerson CT, Smith SJ, Haines JH. 1986. An annotated catalog of the Pyrenomycetes. Described by Charles H. Peck. *Bulletin of the New York State Museum* 459: 1–74.
- Bitzer J, Læssøe T, Fournier J, Kummer V, Decock C, et al. 2008. Affinities of Phylacia and the daldinoid Xylariaceae, inferred from chemotypes of cultures and ribosomal DNA sequences. *Mycological Research* 112: 251–270.
- Clements FE, Shear CL. 1931. *Genera of fungi*. Edn 2. i–vii, 1–496, 58 plates. Wilson Company, New York, USA.
- Currey F. 1859. Synopsis of the fructification of the compound Sphaeriae of the Hookerian herbarium. *The Transactions of the Linnean Society of London* 22: 257–287, pl. 45–49.
- Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
- Ellis JB, Everhart BM. 1892. *The North American Pyrenomycetes*. Newfield, NJ.

- Fournier F, Lechat C. 2011. *Eutypella phaeospora*, a new species on Chenopodiaceae. *Mycotaxon* 118: 441–446.
- Francis SM. 1975. *Anthostomella* Sacc. (Part I). *Mycological Papers* 139: 1–97.
- Fries EM. 1823. *Systema Mycologicum* 2, 2: i, 275–620. Lund, Sweden.
- Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis. program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Haynes JD. 1969. The developmental morphology of *Anthostoma gastrinum*. *Mycologia* 61: 518–525.
- Hoog GS de, Gerrits van den Ende AHG. 1998. Molecular diagnostics of clinical strains of filamentous basidiomycetes. *Mycoses* 41: 183–189.
- Hsieh H-M, Ju Y-M, Rogers JD. 2005. Molecular phylogeny of *Hypoxylo* and closely related genera. *Mycologia* 97: 844–865.
- Hsieh H-M, Lin C-R, Fang M-J, Rogers JD, Fournier J, Lechat C, Ju Y-M. 2010. Phylogenetic status of *Xylaria* subgenus *Pseudoxylaria* among taxa of the subfamily *Xylarioideae* (*Xylariaceae*) and phylogeny of the taxa involved in the subfamily. *Molecular Phylogenetics and Evolution* 54: 957–969.
- Jaklitsch WM. 2009. European species of *Hypocrea* – Part I. *Studies in Mycology* 63: 1–91.
- Jaklitsch WM, Stadler M, Voglmayr H. 2012. Blue pigment in *Hypocrea caerulescens* sp. nov. and two additional new species in sect. *Trichoderma*. *Mycologia* 104: 925–941.
- Jaklitsch WM, Voglmayr H. 2011. *Nectria eustromatica* sp. nov., an exceptional species with a hypocreaceous stroma. *Mycologia* 103: 209–218.
- Ju Y-M, Rogers JD. 1996. A revision of the genus *Hypoxylo*. *Mycologia Memoirs* 20: 1–365.
- Ju Y-M, Rogers JD. 1999. The *Xylariaceae* of Taiwan (excluding *Anthostomella*). *Mycotaxon* 73: 343–440.
- Ju Y-M, San Martín F, Rogers JD. 1993. Three *xylariaceae* fungi with scoliosporous conidia. *Mycotaxon* 47: 219–228.
- Katoh K, Misawa K, Kuma K, Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066.
- Katoh K, Toh H. 2008. Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* 9: 286–298.
- Kornerup A, Wanscher JH. 1981. *Taschenlexikon der Farben*. Muster-Schmidt Verlag, Zürich-Göttingen.
- Læssøe T. 1994. *Index Ascomycetum* 1. *Xylariaceae*. *Systema Ascomycetum* 13: 43–112.
- Læssøe T, Spooner BM. 1994. *Rosellinia* & *Astrocystis* (*Xylariaceae*): new species and generic concepts. *Kew Bulletin* 49: 1–70.
- Liu YL, Whelen S, Hall BD. 1999. Phylogenetic relationships among ascomycetes: evidence from an RNA polymerase II subunit. *Molecular Biology and Evolution* 16: 1799–1808.
- Lu BS, Hyde KD. 2000. A world monograph of *Anthostomella*. *Fungal Diversity Research Series* 4: 1–376. Fungal Diversity Press, Hong Kong.
- Martin PMD. 1969. Studies in the *Xylariaceae*: VII. *Anthostomella* and *Lopadostoma*. *Journal of South African Botany* 35: 393–410.
- Martin PMD. 1976. Studies in the *Xylariaceae*: supplementary note. *Journal of South African Botany* 42: 71–83.
- Mathiassen G. 1993. Corticolous and lignicolous pyrenomycetes on *Salix* along a mid-Scandinavian transect. *Sommerfeltia* 20: 1–180.
- Müller E, Arx JA von. 1962. Die Gattungen der didymosporen Pyrenomyceten. *Beiträge zur Kryptogamenflora der Schweiz* 11, 2: 1–922.
- Nannfeldt JA. 1972. *Camarops* Karst. (*Sphaeriales-Boliniaceae*) with special regard to its European species. *Svensk Botanisk Tidskrift* 66: 335–376.
- Nitschke TRJ. 1867. *Pyrenomycetes Germanici*. Die Kernpilze Deutschlands bearbeitet von Dr. Th. Nitschke 1: i–ii, 1–160. Eduard Trewendt, Breslau.
- Oth G. 1863. Vierter Nachtrag zu dem in Nr. 15–23 enthaltenen Verzeichniss schweizerischer Pilze. *Mittheilungen der Naturforschenden Gesellschaft in Bern* Nr. 531–552: 70–90.
- Oth G. 1868. Sechster Nachtrag zu dem in Nr. 15–23 enthaltenen Verzeichniss schweizerischer Pilze. *Mittheilungen der Naturforschenden Gesellschaft in Bern* Nr. 654–683: 37–70.
- Oth G. 1870. Siebenter Nachtrag zu dem in den Mittheilungen vom Jahr 1844 enthaltenen Verzeichnisse schweizerischer Pilze, und Fortsetzung der Nachträge vom Jahr 1846, 1857, 1863, 1865 und 1868. *Mittheilungen der Naturforschenden Gesellschaft in Bern* Nr. 711–744: 88–115.
- Petrak F. 1923. *Mykologische Notizen* VI. *Annales Mycologici* 21: 182–335.
- Rappaz F. 1992. *Anthostoma decipiens* et sa position systématique. *Mycologia Helvetica* 5: 21–32.
- Rappaz F. 1993. Germination conidienne des *Diatrypales*: rôle du substrat et de l'inoculum mis en évidence chez *Anthostoma decipiens*. *Sydowia* 44: 294–306.
- Rappaz F. 1995. *Anthostomella* and related *xylariaceae* fungi on hard wood from Europe and North America. *Mycologia Helvetica* 7: 99–168.
- Saccardo PA. 1882. *Sylloge Fungorum* 1: 1–768.
- Saccardo PA. 1895. *Sylloge Fungorum* 11: 1–753.
- San Martín González F, Lavin PA. 1997. Los ascomycetes *Acanthonitschka*, *Corynelia*, *Lopadostoma* y *Camarops* en México. *Acta Botánica Mexicana* 41: 31–41.
- Schranz JP. 1960 ('1961'). Recherches sur les pyrenomycètes de l'ordre des *Diatrypales*, sensu M. Chadeffaud, 1957. *Bulletin trimestriel de la Société mycologique de France* 76: 305–407.
- Silvestro D, Michalak I. 2012. raxmlGUI: a graphical front-end for RAXML. *Organisms Diversity & Evolution* 12: 335–337.
- Stamatakis E. 2006. RAXML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- Swofford DL. 2002. PAUP\* 4.0b10: phylogenetic analysis using parsimony (\*and other methods). Sinauer Associates, Sunderland, Massachusetts.
- Thiers B. 2013. *Index Herbariorum*: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>.
- Traverso GB. 1906. *Flora Italica Cryptogama*. Pars 1: *Fungi*. *Pyrenomycetae*. *Xylariaceae*, *Valsaceae*, *Ceratostomataceae* 2: 1–352. Società Botanica Italiana, Rocca S. Casciano, Italy.
- Vasilyeva LN, Scheuer C. 1996. Neuere Aufsammlungen stromatischer Pyrenomyceten aus Österreich, insbesondere der Steiermark. *Mitteilungen des naturwissenschaftlichen Vereins der Steiermark* 126: 61–82.
- Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* 172: 4238–4246.
- Voglmayr H, Jaklitsch WM. 2008. *Prosthecium* species with *Stegosporium* anamorphs on *Acer*. *Mycological Research* 112: 885–905.
- Voglmayr H, Jaklitsch WM. 2011. Molecular data reveal high host specificity in the phylogenetically isolated genus *Massaria* (Ascomycota, *Massariaceae*). *Fungal Diversity* 46: 133–170.
- Voglmayr H, Rossman AY, Castlebury LA, Jaklitsch WM. 2012. Multigene phylogeny and taxonomy of the genus *Melanconiella* (*Diaporthales*). *Fungal Diversity* 57: 1–44.
- Werle E, Schneider C, Renner M, Völker M, Fiehn W. 1994. Convenient single-step, one tube purification of PCR products for direct sequencing. *Nucleic Acids Research* 22: 4354–4355.
- White TJ, Bruns T, Lee S, Taylor J. 1990. Amplified and direct sequencing of fungal ribosomal RNA genes for phylogenies. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds), *PCR protocols: A guide to methods and applications*: 315–322. Academic Press, San Diego.