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. lachati*, *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 ailanthi, 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. pouzani* and *Barmaelia macrosora* 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* (*Diatype*) adusta.

**Article info**

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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 *Anthostomella* 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*. Lassee (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 Lassee & 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 *Barmaelia* for species similar to this subgenus, but with inamylloid ascus apices and ascospores that tend to be allantoid, i.e. being closer to the *Diatrypaceae*. Lassee & 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 elipsoid 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 *Helicogermisla* and *Leptomassaria*, which differ by spiralling ascospore germ slits, *Helicogermisla* also by the absence of an apical apparatus. *Barmaelia* differs mostly by inamylloid 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 synonyms other than those of official culture collections (Centralbureau 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...
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; Crel 2009) 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) 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 ± 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 SZ60 or Nikon SMZ1500 and Nomarski differential interference contrast (DIC) using the compound microscope Nikon Eclipse E600. Kornerup & Wanscher (1981) was used as the colour standard.

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

| Taxon                        | strain*    | host                    | GenBank accesses |
|------------------------------|------------|-------------------------|------------------|
| Anthostoma decipiens         | CD         | Carpinus betulus        | KC774565         |
| Barmaella macrospora         | BM         | Populus cf. nigra       | KC774566         |
| Cryptovalsa rubenhorati      | CreL       | Hippocrepis emerus      | KC774567         |
| Lopadostoma americarum       | CBS 133211 = LGB* | Quercus sp. (white oak) | KC774568, KC774525 |
| Lopadostoma cf. amoenum      | MUCL 51842 = LA | Fagus sylvatica       | KC774569         |
| Lopadostoma dryophilum       | CBS 133213 = LG21* | Quercus petraea       | KC774570, KC774526 |
|                             | LG23       | Quercus petraea         | KC774571, KC774527 |
|                             | LG24       | Quercus petraea         | KC774572, KC774528 |
|                             | CBS 107.39 = LG41 | n. a.                   | KC774573, KC774529 |
| Lopadostoma fagi             | LF         | Fagus sylvatica         | KC774574         |
|                             | CBS 133206 = LF1* | Fagus sylvatica       | KC774575, KC774531 |
|                             | LF2        | Fagus sylvatica         | KC774576         |
|                             | LF5        | Fagus sylvatica         | KC774577         |
|                             | LG2        | Corylus avellana        | KC774578         |
| Lopadostoma gastrinum        | LG1        | Carpinus betulus        | KC774579         |
|                             | LG18       | Prunus padus            | KC774580         |
|                             | CBS 133210 = LG2 | Ulmus glabra           | KC774581, KC774536 |
|                             | LG20       | Carpinus betulus        | KC774582         |
|                             | LG26       | Ulmus minor             | KC774583         |
|                             | CBS 134632 = LG4* | Ulmus minor            | KC774584, KC774537 |
|                             | LG5        | Ulmus minor             | KC774585, KC774538 |
|                             | LG6        | Acer campestrae         | KC774586         |
|                             | LG7        | Acer campestrae         | KC774587         |
| Lopadostoma insulare         | LG32       | Quercus coccofera      | KC774588, KC774541 |
|                             | CBS 133214 = LQM* | Quercus ilex           | KC774589, KC774542 |
| Lopadostoma lechatii         | CBS 133694 = LG22* | Carpinus betulus      | KC774590, KC774543 |
| Lopadostoma linopernum       | CBS 133208 = LPL* | Pistacia lentiscus     | KC774591, KC774544 |
|                             | LPL1       | Pistacia lentiscus      | KC774592         |
| Lopadostoma meridionale      | CBS 133209 = LG* | Quercus ilex           | KC774593         |
|                             | LG29       | Quercus ilex            | KC774594         |
|                             | LG33       | Quercus coccofera      | KC774595         |
|                             | LG34       | Quercus coccofera      | KC774596         |
|                             | LG35       | Quercus ilex            | KC774597         |
|                             | LG36       | Quercus ilex            | KC774598         |
|                             | LG40       | Quercus ilex            | KC774599         |
|                             | LG41       | Quercus ilex            | KC774599         |
| Lopadostoma cf. polynesium   | LAG        | Amelanchier ovalis      | KC774600         |
| Lopadostoma pouzarii         | CBS 103.96 = LPO | Fraxinus excelsior     | KC774601, KC774554 |
|                             | MUCL 47149 = LPO1 | Fraxinus excelsior    | KC774602         |
| Lopadostoma quercicola       | CBS 133212 = LG12 | Quercus cerris         | KC774603         |
|                             | LG14       | Quercus petraea         | KC774604         |
|                             | LG15       | Quercus cerris          | KC774605         |
|                             | LG16       | Quercus cerris          | KC774606         |
|                             | LG17       | Quercus petraea?        | KC774607         |
|                             | LG19       | Quercus petraea         | KC774608, KC774557 |
|                             | LG25       | Quercus sp.             | KC774609         |
|                             | CBS 134633 = LG27* | Quercus pubescens     | KC774610, KC774558 |
|                             | LG3        | Quercus suber           | KC774611         |
|                             | LG37       | Quercus cerris          | KC774612         |
|                             | LG38       | Quercus pubescens       | KC774613         |
|                             | LG39       | Quercus cerris          | KC774614         |
|                             | LG9        | Quercus cerris          | KC774615         |
| Lopadostoma turgidum         | LT         | Fagus sylvatica         | KC774616         |
|                             | LT1        | Fagus sylvatica         | KC774617         |
|                             | CBS 133207 = LT2* | Fagus sylvatica       | KC774618         |
|                             | LT3        | Fagus sylvatica         | KC774619         |
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 (QIAgent 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 Diatrypeaceae, showing the phylogenetic position of Lopadostoma spp., Barrmaelia macrospora, Anthostomella 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 *Dia trypaceae* were selected from GenBank; *Hypocrea rufa* and *Nectria cinnabaria* (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 pouzari* as outgroup according to Table 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 (Katoh et al. 2002, Katoh & Toh 2008) implemented in UGENE 1.10.0 (http://ugene.unipr.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 (Swoford 2002), using 1,000 replicates of heuristic search with random addition of sequences and subsequent TBR branch swapping (MULTREES option in effect, COLLAPSE=MAXBRLLEN, 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=MINBRLLEN 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 GTRCAT 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 *Creosphe ria 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. *poly nemium* and *Anthostomelia* cf. *conorum* cannot be drawn. *Lopadostoma pouzari*, *L. cf. amoenum*, *L. cf. poly nemium* and *Barmela mia macros pora* are phylogenetically distinct from *Lopadostoma* s.str. and dispersed among *Xylariaceae* (Fig. 1). *Anthostoma decipiens* and *Cryptovalsa rabenhorstii* are placed within *Dia trypaceae* (Fig. 1).

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 widely 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 *Lopadosto ma* species growing on *Quercus* formed an unsupported (Fig. 1) and highly supported (Fig. 2) monophyly in the analyses of the nuLSU and the combined matrices, respectively. *Lopadostoma gastrinum*, *L. lechatii* and *L. linospernum* 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. linospernum*, which are conspicuously similar in these characters, reside in different clades.

Phenotype

*Lopadostoma* in a strict sense, i.e. as a monophyly, 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*. However, this definition may be too restrictive. 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 concealed 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 pulvinulate, 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.
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) µm 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 µm 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 biseriate 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 epispore
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

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**Fig. 3** *Lopadostoma* cultures at room temperature. a, b. *L. americanum* (b. reverse); c. *L. dryophilum* (LG21); d, e. *L. fagi* (LF1); 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 ± 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. Stromata well delimited, separate or coalescent in small groups, with a visible black line around them easily observable in transverse and vertical section

3. Stromata on *Fagus sylvatica* or *Corylus avellana*...

4. Stromata on other hosts...

5. Ascospores 10.2–12.2 × 5.5–6.0 µm, with unilateral germ slit, on *Fagus*...

6. Ascospores 7.7–9.8 × 3.7–4.2 µm, with circumferential germ slit...

7. On *Carya alba* in North America, ascospores 9.0–11.8 × 4.0–4.7 µm...

8. Stromata on *Quercus* spp. in Europe, ascospores 9.5–12.0 × 4.3–5.0 µm...

9. Stromata internally white to pale-coloured, especially between ostiolar necks...

10. Stromata internally darker-coloured, olivaceous, brown to blackish between ostiolar necks...

11. Ascospores 10.5–12.8 × 4.5–5.5 µm; on *Ulmus* and other hosts but not *Fagus* or *Quercus*...

12. Ascospores 8.0–9.5 × 3.5–4.3 µm; on *Carpinus betulus*...

13. Tissue between ostiolar necks yellow-brown or olivaceous, ascospores large, (12–)13–17.5 × 4.3–6.2 µm...

14. Tissue between ostiolar necks dark brown, dark grey to blackish; ascospores smaller; on *Quercus* spp. ...

15. On *Quercus petraea* and *Q. robur* in temperate Europe...

16. Not on *Quercus*...

17. On *Pistacia lentiscus* in Mediterranean Europe and North Africa...

18. On *Alnus*, known from a single collection in Switzerland; ascospores 12–15 × 4.3–5.5 µm (colour of tissue between ostioles to be verified)...

19. Ascospores 7.2–9.2 × 3.5–4.0 µm, on *Quercus cocifera* and *Q. ilex* on Mediterranean islands...

20. Ascospores averaging larger, 9.2–12.8 × 3.5–5.0 µm...

21. On white oaks, e.g. *Quercus alba*, in North America; ascospores 9.2–11.5 × 3.5–4.2 µm...

22. On other species of *Quercus*, in Europe...

23. On *Quercus cocifera* and *Q. ilex*; ostioles umbilicate in the disc; ascospores 10.3–12.8 × 4.0–4.8 µm; forming a largetella-like asexual morph in culture...

24. On *Quercus cerris*, *Q. petraea*, *Q. pubescens* and *Q. suber*, possibly also *Q. robur*; ostioles typically papillate; ascospores 9.5–12.0 × 4.3–5.0 µm; not forming an asexual morph in culture...

**SPECIES DESCRIPTIONS**

Descriptions of accepted species are given in alphabetical order.

### Lopadostoma ailanthi (G.H. Otth) Jaklitsch, J. Fourn. & Voglmayr, sp. 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 Steflsburg, in a garden, on a dead twig of *Allanthus altissima* (given as *Allanthus 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 × 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; ostioles necks long, convergent in the disc. *Asci* cylindrical, containing 8 uniseriate ascospores, apical ring flat, amyloid, (1.8–)2–3.2 (–2.5) µm wide and (0.4–) 0.6–0.9 µm high (n = 15). *Ascospores* oblong or narrowly ellipsoidal, (10.5–)11.7–15.0 (–16.5) × (4.0–)4.3–5.5 (–6.0) µm, 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 *Allanthus 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 *Diatypella 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, paler-coloured and ring-pored, which confirms *Allanthus, 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* (Curt.) 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 = LG6).

*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, project¬ing 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, postulate-erumpent, separate, scattered, rarely in contact, subglobose, 2–3 mm diam, delimited from surrounding bark by a black carbonized line; the latter 80–120 µm 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...
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) × (5.0–)6.0–7.5(–8.3) µm (n = 34), sometimes fusiform due to partly overlapping biseriate or oblique ascospores, flat amyloid apical ring (1.3–)1.5–1.8(–2.0) µm diam, 0.5–0.7(–0.8) µm 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) × (3.3–)3.5–4.2(–4.7) µm, 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 (WU32033, 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 (Curt.) 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 (Curt.) Sacc. var. minor Cke. (1876; Grevillea V, p. 32, pl. 75/13 as Diatypo 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 stroma, 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 asc 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, I/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 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. Phaeospora dryophilum G.H. Otth, Mitt. Naturf. Ges. Bern Nr. 654–683: 42. 1888.
  = Sphaeria (Diatype) 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 (Curt.) Sacc., Syll. Fung. 1: 308. 1882.
  = Lopadostoma morthieri (Fuckel) Schratt., Bull. Trimestriel Soc. Mycol. France 76: 370. 1963 (publ. 1961).
  = Quaternaria morthieri Fuckel, Jahlrb. Nassauischen Vereins Naturk. 23–24: 229. 1870 (1869–1870).

Holotype of the basionym Phaeospora dryophilum. SCHWITZERL. BERN, Bremgartenwald, on Quercus sp. (Q. petraea or Q. robur), no date given, (B 70 00114745; as Valsa tumida). Epitype here designated: AUSTRIA, Nieder-österreich, Gießhübl-Perchtoldsdorf, on branches of Quercus petraea, old Diatypella quercina and Enchona interna, 25 Mar. 2012, H. Voglmayr (WU 332035; ex-epitype culture CBS 133213 = LG21; MBT175915).

Ecotrophic 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 stroma in case of widely erumpent entire stroma) pusillate, 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 dark 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. Asc I long cylindrical, variably stipitate, containing (6–)8 uniseriate, sometimes partly biseriate or obliquely overlapping ascospores, spore size (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, I/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 pulvinate but no conidia formed.

Distribution & Habitat — Europe, in corticated branches of Quercus petraea and probably Q. robur. Apparently common in Western Europe.

Other specimens examined, FRANCE, Ariège, Rimont, Las Muros, on branch of Quercus petraea, 30 Aug. 2009, J. Fournier JF 09223 (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 33063; culture LG23); Rimont, Saunier, elev. c. 450 m, on bark of Quercus petraea, 21 Nov. 2008, J. Fournier JF 08196; Pyrénées-Atlantiques, Oloron, Prélachon-Josbaig, Bois de Josbaig, Quercus cf. petraea. — GERMANY, Hessen, Oestrich-Winkel, Vorderwald, no date given, Fuckel, on branch of Quercus petraea (G 0011565, as Quaternaria morthiei). — SPAIN, Asturias, Soto de Los Infantes, near Viescas, on branches of Quercus petraea, W. Jaklitsch & H. Voglmayr (WU 32097). — SCHWITZERL, Jura mountains, near Neuchâtel, on branch of Quercus cf. petraea, 28 Apr. 1857, P. Morthier, teste G. Colomb-Duplan (G 0011566, as Quaternaria morthiei, lectotype of Q. morthiei here selected; MBT175914); ibid., 15 Nov. 1867, P. Morthier (G 0011563, as Quaternaria morthiei); ibid., Mar. 1871 (G 0011564, as Quaternaria morthiei). — 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, m–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-
spernum* 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 dry-
ophilum* 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. How-
ever, 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 Scandinavum*, while the 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 Scandinavum* 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. How-
ever, *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 gregari-
ous, separate or coalescent, flattened pustules 1–2 mm diam, sli-
ghtly raising the peridium, discolouring it dark silvery grey
above the pustules, contrasting with the surrounding reddish
brown colour. Pustules pierced at their centre by a dull black
ecostromatic disc 0.37–0.84 mm in its greatest dimension
(av. = 0.53 mm, n = 90), circular or elliptic, flat, slightly con-
 vex or convex, projecting 120–250 µm above the peridium,
surrounded by teeth-like remnants of the ruptured peridium,
sometimes containing distinctly papillate ostiolyse. Tissue
between the ostiolyse blackish, soft-textured, tissue surround-
ing 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 felly layer spreading over the
wood surface. Perithecia (3–)6–8 in a cluster, monostichous,
circinate, flasch-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 uniloculate,
inconspicuous. Asci cylindrical, spore-bearing part (53–)64–
79(–83) × (5.0–)5.3–6.0(–7.0) µm (n = 31), with 8 uniseri-
ate ascospores; apical ring (1.6–)1.9–2.2(–2.5) µm wide,
(0.6–)1.0–1.1(–1.3) µm high (n = 35). Ascospores oblong or nar-
rowly 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 ‘chemi-
cal’, 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 nar-
rowly 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*.

Other specimens 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); Zabred, 18 Aug. 1996, W. Jaklitsch W.J. 923 (WU 32100); Niederösterreich, Hainbuch, grid square 7763/1, 28 Sept. 1996, W. Jaklitsch; Mauerbach, grid square 7764/2, 16 May 1992, W. Jaklitsch W.J. 25 (WU 32098); Weidling-
bach, 3 Mar. 2012, W. Jaklitsch & H. Voglmayr (WU 32041; culture LF3); Steiermark, Berghausen, Grafenitzberg, grid square 9259/4, 20 Sept. 1996, Kösch, 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 8760/6, 12 Sept. 2002, W. Jaklitsch. — FRANCE, Ariege, 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. Schöller, 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. turgi-
dum*, but differ in slightly larger ectostromatic discs that may
contain distinctly papillate ostiolyse, smaller, particularly nar-
rower 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.
**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 towards 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), white to yellowish, becoming greyish brown to black from the centre, odour indistinct; no asexual morph formed. *Perithecia* reverse whitish to yellowish, becoming greyish brown to black.

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

**Other specimens examined.** *Austria*, Burgenland, Bad Sauerbrunn, Himrer 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); Großenzersdorf, Lobau, grid square 7865/1, on branch of *Ulmus minor*, 27 Feb. 2000, W. Jaklitsch; Hagernbrunn, Bisamberg-east side, grid square 7664/3, on branch of *Carpinus betulus*, 30 Oct. 1999, W. Jaklitsch; Vienna, 13th district, Schönbrunner-Gloriette, grid square 7863/2, on branch of *Acer campestre*, 26 Feb. 2003, W. Jaklitsch J.W. 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 Pannonzalacke, grid square 7865/1, on branch of *Ulmus minor*, 4 May 1996, W. Jaklitsch J.W. 852 (WU 32101); ibid., on *Ulmus minor*, 9 Mar. 2002, W. Jaklitsch J.W. 1658 (W); ibid., on *Ulmus minor*, 30 Apr. 2003, W. Jaklitsch J.W. 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*, Arlege, Rimont, Las Muros, on branch of *Acer campestre*, 14 Mar. 2004, J.Fournier JF 1116 (WU 32048; culture LG9); ibid., on branch of *Ulmus minor*, 9 Nov. 2011, J. Fournier JF 1116 (WU 32047; culture LG5); ibid., on branch of *Acer campestre*, 12 Nov. 2011, J. Fournier JF 11170 (WU 32049; culture LG7). — *Greece*, Mikra, Liapades, on branch of *Ulmus minor*, 20 Apr. 2012, W. Jaklitsch (WU 32053); Skippero, 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-Kopa, on *Ulmus sp.*, 17 Nov. 1963, J. Kochman (NY; Mycotheca Polonica, fasc. XIV, no. 343). — *Spain*, Catahula, Val d’Aran, Puerto de Bonaiagua, elev. c. 2 000 m, on branch of *Sorbus chaemaspisius*, 16 May 1986, P. Candousau (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 superfluous, which made a morphological delimitation of other species difficult in the pre-molecular era. Stromata development and ostioles are much dependent on climatic 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 MB803808; Fig. 9

*Holotype.* Spain, Islas Baleares, Mallorca, Es Capdella, between Cami 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 = LGM).

**Etymology.** Occurring on islands.

**Ectostromatic 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 incombustible 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, frequently lying in wet grass, 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 = 36), with 8 uniseriate ascospores, sometimes oblique or biseriate 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.
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 cocifera, 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 ostioli 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; isolecotypes 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 µm 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 volsoid 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) × (5.7–)6.0–7.5(–9.0) µm (n = 40), containing 8 uniseriate, material named as often distinctly overlapping ascospores; apical apparatus short, semiglobose, 4.5–5.5 µm wide, 2.5–3 µm high, containing a refractive, amyloid, (1.6–)1.8–2.2(–2.3) µm wide and (0.4–)0.5–0.8(–1.0) µm 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. Ectostromatic discs; c, d. transverse stroma sections (c. ostiolar level); e–h. vertical stroma sections; i–l. asci (i. in Lugol); m–o. apical ascus 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 µm; k = 10 µm; n–r = 5 µm.
Lopadostoma lechatii Jaklitsch, J. Fourn. & Voglmayr, sp. nov. — MycoBank MB803807; Fig. 10

Holotype. FRANCE, Poitou-Charentes, Deux Sèvres, Villiers en Bois, La Taille, 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 elliptic in outline, black, often with flaps of peridium 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 perithelial groups. Tissue between ostiolar necks whitish or yellowish, woody; tissue around and beneath perithecium 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 volsellate 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 (63–87–80–(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, ellipsoidal, 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 (5C(D3–)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.

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

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

— Anamorph: Lopadostoma linospermum (Durieu & Mont.) Sacc., Syst. Mycol. 1: 305. 1882.

Typification. The type folder of Sphaeria linosperma Durieu & Mont. in PC consists of three species, with the following information: ALGIER, 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 linosperma. PC0085764 (= MC6870) and PC0085765 (= MC8669 = MS424299) are isolateypes. Epitype here designated: TAU, 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 elliptic 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 papillose, 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 perithecium, turning whitish and progressively merging with the basal tissue which is composed of slightly bleached bark tissue. Perithecia 4–20 per stroma, in volsellate 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 round, (6.3–)6.8–8.5–(9.5) µm, ellipsoidal to short cylindrical, with (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 round, (6.3–)6.8–8.5–(9.5) µm, ellipsoidal to short cylindrical, with (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 round, (6.3–)6.8–8.5–(9.5) µm, ellipsoidal to short cylindrical, with (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 round, (6.3–)6.8–8.5–(9.5) µm, ellipsoidal to short cylindrical, with (1.6–)2.0–2.4–(2.6) µm wide, (0.5–)0.6–1.1–(1.2) µm high (n = 33).
**Fig. 11** *Lopadostoma linospermum*. 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 warty 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 cortic- teric branches of *Pistacia lentiscus* in the Mediterranean region.

*Other specimens examined. S Pan, Andalucia, Alcalá de los Gazules, San- tuario de Nuestra Senora de los Santos, N36°26'25.9", W5°48'16.5", on branch of *Pistacia lentiscus*, 17 Mar. 2011, W. Jaklitsch & H. Voglmayr (WU 32061; culture LPL2); Andalucia, 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 char- acteristics 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 stroma- ta of *L. linospermum* often resemble those of a *Diatrypella*.

*Lopadostoma meridionale* Jaklitsch, J. Fourn. & Voglmayr, sp. nov. — MycoBank MBB803809; 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 elliptoid, 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 perithecium dull brownish with whitish spots, composed of slightly bleached bark tissue and whitish hyphae. *Perithecium* 3–10 per stroma, arranged in vasooid 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. *Ascii* cylindrical, spore port (68–)74–95–(113) x (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, some- times reniform or banana-shaped, (8.7–)10.3–12.8–(14.8) x (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, turn- ing 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 in mucous, yellow to orange, brown to black drops or pustules. Conidia falcate, (19–)22–27–(30) x (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 cocciifera* and *Q. ilex*, widely distributed, particularly in the Mediterranean region.

*Other specimens examined. Croataia, Istria, Rovinj, holm oak wood NW Mursena, on a branch of *Quercus ilex*, 17 May 2012, H. Voglmayr (WU 32068; culture LG36); Ugiljan, 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 60807 (WU 32063; culture LG10) — Greece, Corfu, Agia Anna, on branch of *Quercus cocciifera*, 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 cocciifera*, 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 interme- diate 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 MBB803810; 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 less or less long rows at the bottom of cracks in thick bark, grey or black, usually not surrounded by ruptured periderm, circular or elliptic 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 contain- ing several perithecial groups; the latter subglobose, usually not delimited by a black stomatic 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
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, I/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

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**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, o: 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.
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 10–15(–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. robur, possibly also Q. robur; widely distributed, particularly common around Vienna, Austria.

Other specimens examined (all on corticated branches), AUSTRIA, Niederösterreich, Gießhübel, 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 CG 18, Mar. 2012, H. Voglmayr & W. Jaklitsch (WU 32074; culture LG15); Waneck, NE Pernitz, near Schutzhaus, on Quercus petraea, 9 June 2013, H. Voglmayr & I. Greilhuber (L); Vienna, 19th district, Hermannskogel, grid square 7763/2, on branch of Quercus cerris, 11 Feb. 1995, W. Jaklitsch WJ. 489 (WU 32104); ibid., on Quercus cerris, 19 Aug. 1995, W. Jaklitsch WJ. 710 (WU 32105); ibid., on Quercus cerris, 27 Mar. 1995, W. Jaklitsch WJ. 1254 (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 WJ. 987 (WU 32106); CROATIA, Istria, Rovinj, at the road Rovinj-Bale, c. 2 km W Balle, 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); Vatinana, NW Žureči, at the road to Ponie Porton, on Quercus cerris, 20 May 2012, H. Voglmayr (WU 32082; culture LG39); France, Côte d’Or, forêt de Longchamp, near Maison Forestière du Terre, elev. 240 m, on Quercus sp. (Q. petraea or Q. robur), 13 Oct. 2005, P. Leroy PL054314D; Indre et Loire, Bois de Roche-Monts, on Quercus sp. (Q. petraea or Q. robur), 30 May 2006, P. Leroy PL062262C (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, Sardegna, Aggius, on branch of Quercus suber, 7 Nov. 2009, W. Jaklitsch (WU 32070; culture LG33) – 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. Stroma of this species are often widely erumpent and contain many perithecia 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-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, 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.) Nitsche, Pyrenomycetes 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 perr nzend and discoloring it dark silvery grey above the pustules, contrasting with the surrounding red-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 stroma seated on a thick dark brown felly layer spreading over the wood surface. Perithecium 3–8(–10) per stroma, monostichous, cinerate, 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. Ostioli 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. Conidia 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. ektostromatic 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, 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*, Kämmten, St. Margareten im Rosental, Starwald, 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., Zabrde, 12 Aug. 1995, W. Jaklitsch; Rechberg, grid square 9453/5, 6 Sept. 1998, W. Jaklitsch; Niederösterreich, Hainbuch, grid 7763/3, 28 Sept. 1996, W. Jaklitsch; Lahnsettel, virgin forest Neuwald, from Donaudorf, grid square 8259/1, 31 July 1999, W. Jaklitsch; Lunz am See, Rothwald 2, grid square 8256/2, 3 July 1999, W. Jaklitsch; Maurabach, 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, GrazSchutz, grid square 9295/4, 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 7832/2, 15 Dec. 1998, W. Jaklitsch; Cobenzl, grid square 7762/5, 7 July 1998, W. Jaklitsch W.J. 1172 (WU 32109); 23rd district, Maurer Wald, grid square 7863/1, 3 Oct. 1998, W. Jaklitsch. – *France*, Ariège, PratCommunal, Loumet, elev. 900–950 m, 21 Apr. 2012, J. Fournier JF 12051; Rimont, Las Murors, 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 turdicum* is common on *Fagus* in Europe, but is at times locally nearly entirely replaced by *L. fagi*, which differs in slightly larger eктостromatic discs (0.5 vs 0.3 mm wide; 0.2–0.3 mm high, surrounded by decayed cortical tissue; black stromatic line absent). *Ostiora* necks central or more commonly eccentric and oblique. *Paraphyses* simple, abundant. Asc cylinindrical, 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 Laessë & Spooner (1994) except for slightly smaller ascospores. Laessë & 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. (Norimbegiae) 2: 778. 1833).

Current name — *Apiorhynchospora 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 peritheciun 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 µm; f, r, s = 10 µm; h, q = 25 µm; k–m, t = 15 µm; n, o = 0.2 mm.
Lopadostoma conorum (Fuckel) P.M.D. Martin, J. S. African Bot. 42, 1: 75. 1976.

Basionym. Amphiphorea 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 cubiculare Fr., Syst. Mycol. (Lundae) 2, 2: 477. 1823.

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

Current name — Helicogersmita fleischhakii 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 valvoid perithecia and ascospores 12–15 × 4–6 μm. 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 0.4–1.6 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. Ascii cylindrical, spore part (72–)75–88(–92) × (6.0–)6.3–7.3(–7.5) μm (n = 10), containing 8 uniseriate ascospores and a flat refractive, amyloid ring. Ascospores oblong, (9.7–)10.0–11.8(–14.8) × (4.0–)4.3–5.2(–5.5) μm, l/w (1.9–)2.1–2.6(–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–)7.8–10.5(–12.2) × (2.5–)2.7–3.3(–3.5) μm, l/w = (2.1–)2.5–3.7(–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 (43–50 × 14–17 μm) having a spiralling germ slit.

Lopadostoma helvetica (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 massareae (De Not.) Traverso, Fl. Ital. Crypt. 1, 1, 1: 172. 1906.

Basionym. Hypoxylon massareae De Not., Sfcr. Ital.: 17. 1863.

In corticated branches in Northern Italy, with a black stromatic line and dark disc; ascospores 20 × 8 μm. According to A. Granit (pers. comm.) the species is indicated on the handwritten label of the sole specimen present in RO, as “Sphaeria Massareae DNtr a Valtellina. Dr. Balsamo a Massara lecta 1836”. Unfortunately no response was obtained from RO, the name Lopadostoma massareae 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 which may eventually be split into several genera.

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

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

This is Coniochaeta cf. ligniaria 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 Helicogersmita 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 accordance with the description of L. polynesium by Rappaz (1995), was kindly provided by Alain Gardiennet: France, 21, Côte-d’Or, Savginy-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 clypsyus (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 (contain rose 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. Pettrini, 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 A 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. Fucella rhenana Fuckel, Jahrb. Nassausischen Vereins Naturk. 23–24: 224. 1870 (1869–1870).

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

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

Basionym. Anthostoma saphrophilum 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). Læssee & Spooner (1994) interpreted this fungus as a Helicogermslita sp.; see also Barr et al. (1996).

Lopadostoma taeniiosporum (Sacc.) Traverso, Fl. Ital. Crypt., Pars 1: Fungi. Pyrenomycetaceae, Xylariaceae, Valasaceae, Ceratostomataceae 1, 1: 171. 1906.

Basionym. Anthostoma taeniiosporum 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 = 1.4–1.6(–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. taeniiosporum 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. Lokuloaomits. 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 Spieg., Boll Acad. Nat. 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, Pyrenomycetes Germanici 1: 111. 1867.

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

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

= *Cryptosphaeria decipiens* (Lam. & DC.) Lassèe & 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 accesses 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) 177726), 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–)5.5–6.0–(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 ascii. 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 melanositus*, presently a synonym of *Barrmaelia oxyacanthae* (see Mathiassen 1993: 65), Rappaz (1995: 137) or Lassèe & 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 insidiosa* P. Crouan & H. Crouan, *Florule Finistère*: 32. 1867.

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

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 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* cylindric, 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), uniseriate, (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, Finistere, on bark of *Fagus sylvatica*, 6 June 1868, *Crouan* (holotype; CO), kindly provided by J.P. Priaux.

Notes — Morphological characters including ascospore and ascus plug morphology are in agreement with *Anthostomella (Diatrype) adusta*; see also Lassèe & Spooner (1994: 44). Rappaz (1995: 148) and Barr et al. (1986: 6) for descriptions of *A. adusta*. Lassèe & 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. *Anthostomella insidiosa* 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 ascus plug exclude this fungus from *Lopadostoma*.

**Anthostoma phaeospermum** (Ellis) Sacc., *Syll. Fung.* II: 14. 1883.

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

An examination of the holotype (USA, Iowa, branches of *Amelanchier canadensis*; NY) confirmed 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. 6. 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 *Enchkoa 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*, *Eupexylinx*, *Helicogermisla*, *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 *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 homoplasys and thus low power of resolution (LSU), or poor alignment 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. polyneum* 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 Hypoxylon (Hsieh et al. 2005) and in *Xylaria* (Hsieh et al. 2010), but they are only available for a 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 Corsu, 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. linospermum* and *L. dryophyllum*, 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 stromal 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. turdigum*) by San Martín & Lavin (1997) from *Quercus* sp. in Mexico with small ascospores (8–9.5(–11) × 3.5–4 μm). Such concentration of bark-inhabiting species on a certain host genus is conspicuous, as other genera of similar ecology, e.g. *Massaria* and *Prosthecium* (Steinporium) on *Acer* (Voglmyar & Jaklitsch 2008, 2011) and *Melanconia* on *Carpinus* and the closely related genus *Ostrya* (Voglmyar 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*, *L. fagi* and *L. turdigum*, may be also common in summer, depending on moisture.

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