



The genus *Elaphomyces* (Ascomycota, Eurotiales): a ribosomal DNA-based phylogeny and revised systematics of European ‘deer truffles’

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Key words

Astraeus
Eurotiaceae
Eurotiomycetes
identification key
nomenclature
Pseudotulostoma
rDNA phylogeny
Rhizopogon
taxonomy
Terfezia

Abstract *Elaphomyces* (‘deer truffles’) is one of the most important ectomycorrhizal fungal genera in temperate and subarctic forest ecosystems, but also one of the least documented in public databases. The current systematics are mainly based on macromorphology, and is not significantly different from that proposed by Vittadini (1831). Within the 49 species recognised worldwide, 23 were originally described from Europe and 17 of these were described before the 20th century. Moreover, very recent phylogenetic treatments of the genus are mainly based on a few extra-European species and most common European species are still poorly documented. Based on an extensive taxonomic sampling mainly made in the biogeographically rich Cantabrian area (Spain), complemented with collections from France, Greece, Italy, Norway, Portugal and Sweden, all currently recognized species in Europe have been sequenced at the ITS and 28S of the rDNA. Combined phylogenetic analyses yielded molecular support to sections *Elaphomyces* and *Ceratogaster* (here emended), while a third, basal lineage encompasses the sections *Malacodermei* and *Ascoscleroderma* as well as the tropical genus *Pseudotulostoma*. Species limits are discussed and some taxa formerly proposed as genuine species based on morphology and biogeography are re-evaluated as varieties or forms. Spore size and ornamentation, features of the peridial surface, structure of the peridium, and the presence of mycelium patches attached to the peridial surface emerge as the most significant systematic characters. Four new species: *E. barrioi*, *E. quercicola*, *E. roseolus* and *E. violaceoniger*, one new variety: *E. papillatus* var. *sulphureopallidus*, and two new forms: *E. granulatus* forma *pallidosporus* and *E. anthracinus* forma *talosporus* are introduced, as well as four new combinations in the genus: *E. muricatus* var. *reticulatus*, *E. muricatus* var. *variegatus*, *E. papillatus* var. *striatosporus* and *E. moretii* var. *cantabricus*. Lectotypes and epitypes are designated for most recognised species. For systematic purposes, new infrageneric taxa are introduced: *E. sect. Ascoscleroderma* stat. nov., *E. subsect. Sclerodermei* stat. nov., *E. subsect. Maculati* subsect. nov., *E. subsect. Muricati* subsect. nov., and *E. subsect. Papillati* subsect. nov. Lastly, *E. laevigatus*, *E. sapidus*, *E. sulphureopallidus* and *E. trappei* are excluded from the genus and referred to *Rhizopogon roseolus*, *Astraeus sapidus* comb. nov., *Astraeus hygrometricus* and *Terfezia trappei* comb. nov. (syn.: *Terfezia cistophila*), respectively.

Article info Received: 7 June 2016; Accepted: 10 January 2017; Published: 2 June 2017.

INTRODUCTION

The ectomycorrhizal (EcM) genus *Elaphomyces* is a well-known trophic exception within the globally saprobic or pathogenic class *Eurotiomycetes*, order *Eurotiales* (Trappe 1971, LoBuglio et al. 1996, Geiser & LoBuglio 2001, Geiser et al. 2006). Ascomata are hypogaeous, and some species that form voluminous cleistothecia represent a considerable fruiting biomass in

mountain and old-growth coniferous forests (especially *E. granulatus*: Froidevaux & Schwärzel 1977, Vogt et al. 1981, Luoma 1988, Luoma & Frenkel 1991; *E. muricatus*: Bird & McCleneghan 2005; *E. asperulus*: Ławrynowicz et al. 2006). The same species are an important feeding resource for wild mammals, especially rodents (Fogel & Trappe 1978, Currah et al. 2000, Castellano & Stephens 2017) but also bears (Genov 1982) and wild boars (Boudier 1876, Hohmann & Huckschlag 2005, Ławrynowicz et al. 2006), although apparently especially consumed in lean times as secondary food resource (Cork & Kenagy 1989). Anecdotaly, as truffles and many underground vegetal organs, they have been attributed aphrodisiac properties and sold as drugs in the past centuries (Bauhin 1651: 851, Tulasne & Tulasne 1841). Their use of decoctions of *E. muricatus* as a stimulant, for ‘remaining young and treating serious wounds’ in Mexico was reported by Cázares et al. (1992), who also mentioned their use in chamanic practises in association with psychoactive *Psilocybe* species. *Elaphomyces* species can dominate EcM communities, especially in poor, acidic soils (Boudier 1876, Tedersoo et al. 2006, Ishida et al. 2007), and have been reported as especially tolerant to drought (Hawker 1959: 82), what makes them of peculiar interest in the context of global changes regarding old-growth forest resilience and resistance to water stress. Some of the rarer species are also

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Table 1 Sequences analysed in our study. The GenBank accession numbers of sequences generated for the present work are indicated in **bold**.

[illegible]

<i>E. guangdongensis</i>	KH-TW09-031	Herb. pers. A. Paz	Taiwan	18/11/2011	<i>Quercus pyrenaica</i>	HM357250	HM357248
<i>E. hassiacus</i>	IC18111109		Spain, Caceres	25/08/2014		KX238878	KX238878
<i>E. iupperticellus</i>	TH9918		Cameroon	01/09/2014		KT694139	KT694143
<i>E. labyrinthinus</i>	IC13111101	Herb. pers. A. Paz	Spain, Cantabria	13/11/2011	<i>Fagus sylvatica</i>	KX238806	KX238868
<i>E. leonis</i>	IC14111101	Herb. pers. A. Paz	Spain, Cantabria	14/11/2011	<i>Fagus sylvatica</i>	KX238814	—
<i>E. leucosporus</i>	IC26051202	LIP-0001147	Spain, Asturias	26/05/2012	<i>Castanea sativa</i>	KX238815	—
<i>E. leveiliei</i>	IC24051203	Herb. pers. A. Paz	Spain, Cantabria	24/05/2012	<i>Fagus sylvatica</i>	KX238816	—
	IC15031406	LIP-0001148	Spain, Asturias	15/03/2014	<i>Betula pendula</i>	KX238856	—
		MCVE-16960	Italy	03/09/1998		JF907987	—
<i>E. maculatus</i>	IC23071103	LIP-0001149	Spain, Cantabria	23/07/2011	<i>Fagus sylvatica, Corylus avellana</i>	KX238799	—
	IC11061103	Herb. pers. A. Paz	Spain, Cantabria	11/06/2011	<i>Quercus petraea</i>	KX238818	—
	AM36	O-F21188	Norway, Møre og Romsdal	16/09/2011	Broadleaved forest, <i>Corylus</i>	KR029775	KR029775
		MCVE-16961	Italy	13/11/1999		JF907988	—
<i>E. moretii</i> var. <i>moretii</i>	IC14041302	LIP-0001150	France, Moselle	14/04/2013	<i>Pinus</i> sp.	KX238855	—
<i>E. moretii</i> var. <i>cantabricus</i>	IC29041104	Herb. pers. A. Paz	Spain, Asturias	29/04/2011	<i>Castanea sativa</i>	KX238798	—
<i>E. moretii</i> var. <i>echinatus</i>	IC27091306	Herb. pers. A. Paz	Norway, Vest-Agder	27/09/2013	<i>Quercus robur, Tilia cordata, Betula pendula</i>	KX238854	—
		O-21292	Norway, Vest-Agder	27/09/2013	<i>Quercus robur, Picea abies, Betula pendula</i>	KR029779	KR029779
<i>E. muricatus</i> var. <i>muricatus</i>	IC03031214	Herb. pers. A. Paz	Spain, Cantabria	03/03/2012	<i>Pinus radiata</i>	KX238843	—
	IC14041301	Herb. pers. A. Paz	Spain, Asturias	14/04/2013	<i>Castanea sativa, Quercus</i> sp.	KX238847	—
	IC01041301	Herb. pers. A. Paz	Spain, Cantabria	01/04/2013	<i>Eucalyptus globulus</i>	KX238849	—
		O-F245291	Norway, Nordland	11/08/2012	<i>Pinus, Betula</i>	KR029733	KR029733
		K(M)121442	Poland			EU784198	—
			Great Britain		<i>Quercus robur</i>	JF834198	—
<i>E. muricatus</i> var. <i>reticulatus</i>	(as <i>E. sp.</i>)	LIP-0001153	Spain, Cantabria	14/01/2012	<i>Fagus sylvatica, Corylus avellana</i>	KX238851	—
	IC14011206		Spain, Cantabria	03/05/2012	<i>Fagus sylvatica</i>	KX238841	—
	IC03051209		Denmark, Sjælland	06/08/2002		UDB000043	—
<i>E. muricatus</i> var. <i>variegatus</i>	RK02-01	LIP-0001154	Spain, Cantabria	05/01/2013	<i>Fagus sylvatica</i>	KX238850	—
	IC05011307	O-F21007	Norway, Akershus	13/11/2011	<i>Quercus</i> sp.	KX238789	KX238862
	AM152	Herb. pers. A. Paz	Spain, Cantabria	23/07/2011	<i>Fagus sylvatica, Corylus avellana</i>	KX238839	—
	IC23071117	GB-0147062	Sweden, Småland	15/03/2014	<i>Picea abies</i>	KR029730	KR029730
	AM43-2014	O-F245312	Norway, Østfold	09/09/2012	<i>Quercus</i> sp.	KR029736	KR029736
<i>E. aff. muricatus</i>	AM42-2014	O-F245437	Norway, Nord-Trøndelag	08/08/2012	<i>Picea abies</i>	KR029738	KR029738
	AM146	O-F21009	Norway, Akershus	18/11/2011	<i>Quercus robur</i>	KR029739	KR029739
	AM150		Norway, Akershus	19/11/2011	<i>Quercus ?</i>	KR029740	KR029740
	AM151	LIP-0001142	Spain, Asturias	27/11/2011	<i>Castanea sativa, Corylus avellana</i>	KX238824	KX238873
<i>E. mutabilis</i>	IC27111103	Herb. pers. A. Paz	Spain, Cantabria	03/03/2012	<i>Fagus sylvatica</i>	KX238823	—
	IC03031201	LIP-0001136	Spain, Cantabria	12/05/2012	<i>Fagus sylvatica, Corylus avellana</i>	KX238819	KX238872
<i>E. papillatus</i> var. <i>papillatus</i>	IC12051202	Herb. pers. A. Paz	Spain, Cantabria	26/07/2008	<i>Fagus sylvatica, Corylus avellana</i>	KX238801	—
	IC26070803	Herb. pers. A. Paz	Spain, Asturias	26/05/2012	<i>Fagus sylvatica, Castanea sativa</i>	KX238820	—
	IC26051201	Herb. pers. A. Paz	Spain, Cantabria	06/07/2011	<i>Corylus avellana</i>	KX238825	—
<i>E. papillatus</i> var. <i>striatosporus</i>	IC06071105	O-F21185	Norway, Møre og Romsdal	17/09/2011	<i>Corylus avellana</i>	KX238790	—
	AM35	O-F21184	Norway, Nord-Trøndelag	21/10/2011	Rich broadleaved forest, <i>Corylus</i>	KX238794	KX238864
	AM76	O-F245333	Norway, Oslo	21/09/2012	<i>Corylus avellana</i>	KX238861	—
		O-F245330	Norway, Oslo	21/09/2012	<i>Tilia cordata</i>	KR029748	KR029748
		O-F245337	Norway, Oslo	23/09/2012	<i>Corylus, Tilia, Quercus, Betula, Pinus</i>	KR029749	KR029749
<i>E. papillatus</i> var. <i>sulphureopalidus</i>	IC13051212	LIP-0001156	Spain, Asturias	13/05/2012	<i>Castanea sativa, Fagus sylvatica</i>	KX238830	—
<i>E. persoonii</i>	IC15021201	LIP-0001139	Spain, Cantabria	15/02/2012	<i>Fagus sylvatica</i>	KX238829	KX238875
	IC18031201	Herb. pers. A. Paz	Spain, Cantabria	18/03/2012	<i>Fagus sylvatica</i>	KX238828	—
<i>E. quercicola</i>	IC23071107	LIP-0001155	Spain, Cantabria	23/07/2011	<i>Quercus petraea</i>	KX238837	KX238879
	IC23071104	Herb. pers. A. Paz	Spain, Asturias	23/07/2011	<i>Castanea sativa</i>	KX238838	—
<i>E. roseolus</i>	IC02101201	LIP-0001143	Greece, Kastoria	02/10/2012	<i>Carpinus orientalis, Juniperus</i> sp.	KX238845	—
	JMV20140916-1	Herb. pers. A. Paz	Spain, Girona	16/09/2014	<i>Quercus suber</i>	KX238860	KX238871
<i>E. septatus</i>	IC13051213	LIP-0001151	Spain, Asturias	13/05/2012	<i>Castanea sativa, Fagus sylvatica</i>	KX238817	—
	IC10041107	Herb. pers. A. Paz	Spain, Asturias	10/04/2011	<i>Castanea sativa, Fagus sylvatica</i>	KX238807	—
	IC08100621	Herb. pers. A. Paz	Spain, Cantabria	08/10/2006	<i>Fagus sylvatica</i>	KX238808	—
	AM95	O-F21183	Sweden, Gotland	25/09/2011	<i>Quercus, Corylus avellana</i>	KR029776	KR029776
<i>E. spirosporus</i>	IC18121101	LIP-0001152	Spain, Caceres	18/12/2011	<i>Quercus petraea</i>	KX238796	KX238865
<i>E. violaceoniger</i>	IC22021401	LIP-0001135	Spain, Segovia	22/02/2014	<i>Quercus ilex</i>	KX238857	—
	IC15031401	Herb. pers. A. Paz	Norway, Oslo	15/03/2014	<i>Corylus avellana</i>	KX238858	—
<i>E. virgatosporus</i>	AM62	O-F21180	Norway, Møre og Romsdal	17/09/2011	<i>Corylus avellana</i>	KX238793	—

Table 1 (cont.)

Species	Status	Voucher id	Herbarium	Country	Date	Host	ITS	28S
<i>E. virgatosporus</i> (cont.)		IC06031103	Herb. pers. A. Paz	Spain, Asturias	26/03/2011	<i>Castanea sativa</i> , <i>Corylus avellana</i>	KX238802	–
		IC26031101	Herb. pers. A. Paz	Spain, Asturias	26/03/2011	<i>Corylus avellana</i>	KX238809	–
		IC26051213	Herb. pers. A. Paz	Spain, Asturias	26/05/2012	<i>Corylus avellana</i>	KX238811	–
<i>E. sp.</i>		ecm1108 (root tip)		Guyana		<i>Dicymbe corymbosa</i>	JN168718	JN168718
<i>'Pseudotulostoma' volvatum</i>		TH8975		Guyana		<i>Dicymbe corymbosa</i>	JN168735	JN168735
Outgroup								
<i>Aspergillus alliaceus</i>							EF661543	–
<i>Aspergillus arenarius</i>							EU021615	–
<i>Aspergillus clavatus</i>							EF669713	–
<i>Aspergillus peyronelii</i>							LN849398	–
<i>Byssochlamys nivea</i>							DQ322218	–
<i>Geosmithia cylindrospora</i>							AF033386	–
<i>Hamigera fusca</i>							GU092940	–
<i>Hamigera pallida</i>							GU092950	–
<i>Merimbia ingelheimensis</i>							GU092961	–
<i>Penicillium ehrlichii</i>							AF033432	–
<i>Penicillium implicatum</i>							AF033428	–
<i>Penicillium inusitatum</i>							AF033431	–
<i>Penicillium oxalicum</i>							HE651146	–
<i>Penicillium reticulatum</i>							AF033437	–
<i>Penicillium solitum</i>							JX290030	–
<i>Penicillium tularense</i>							AF033487	–
<i>Talaromyces byssochlamydoides</i>							EU021608	–
<i>Talaromyces emersonii</i>							AF033387	–
<i>Thermoascus crustaceus</i>							EU021597	–
Uncultured Eurotiales							KX238810	KX238869

considered as threatened in Central and Northern Europe (Ławrynowicz 2001) or considered to be good indicators of habitat quality (Nitare 2010).

The taxonomic baseline was established by Vittadini (1831) – a famous Italian mycologist who specialised in hypogeous fungi with the aid of trained dogs (Tulasne & Tulasne 1851, Lloyd 1923). Fries (1829) only cited two species (*E. granulatus* and *E. muricatus*), while Vittadini recognised 14 distinct species in 1831 (12 of them as new), and later, 17 (Vittadini 1842), all collected in the Milano area in northern Italy. Tulasne & Tulasne (1841, 1851) added three new species (*E. cyanosporus*, *E. hirtus* and *E. leveillei*) from the Paris area in northern France. Amongst later authors, Hesse (1894), Hollós (1908), Vacek (1949) and Kers (1980, 1984), proposed a few new species in the genus. Revisions reduced a few to synonyms or to lower ranks (Spegazzini 1881, Fontana 1908, 1909). No major revisions and additions have come to light in the 20th century, and no new infrageneric classification has been proposed (Reess & Fisch 1887, Bataille 1921, Hawker 1954, Lange 1956, Ceruti 1960, Eckblad 1962, Moser 1963, Ławrynowicz 1988, 1989, Montecchi & Sarasini 2000). Recently however, three new species have been characterised from north-western Spain, *E. cantabricus* (Paz & Gonzáles 2008), *E. leonis* and *E. spiro-sporus* (Paz et al. 2012).

Meanwhile, extra-European reports of *Elaphomyces* have regularly been made, from South America (Spegazzini 1879), North America (Dodge 1929, Linder 1939, Trappe & Kimbrough 1972, Danielson 1979, Zhang & Minter 1989, Cázares et al. 1992, Castellano et al. 2012b, Beug et al. 2014, Castellano & Stephens 2017), Japan (Imai 1929, 1938, 1939–1940, 1960, Kobayasi 1960), South-Eastern Asia (Corner & Hawker 1953, Zhang 1991), and recently Taiwan (Hosaka et al. 2010), Guyana (Castellano et al. 2012c, 2016), tropical Africa (Buyck et al. 2016, Castellano et al. 2016) and Madagascar (Buyck et al. 2016). Recent investigations in Australia and New Zealand led to the recognition of 16 new species by Castellano et al. (2011, 2012a). Finally, a new and remarkable genus close to *Elaphomyces*: *Pseudotulostoma*, was described from Guyana and Japan (Miller et al. 2001, Asai et al. 2004, Henkel et al. 2006). All these works concur in suggesting that the lineage *Elaphomyces* has an old Gondwanian origin, and current species have a continental or even regional distribution (Castellano et al. 2011, 2012c, 2016, Reynolds 2011). Only very few worldwide distributed species are recognized (if any, possibly recently introduced), contrasting with high regional specific diversity, as described from Europe, Eastern Asia and Australia, and probably overlooked elsewhere, especially in Africa.

Unfortunately, very few molecular data are available to date in the public sequences databases (GenBank, UNITE), and attempts of reconstructing phylogenies at a global scale (Reynolds 2011, Castellano et al. 2016) obviously suffer from the lack of European reference data. Here we aimed at filling this gap, by yielding a first phylogenetic analysis of European *Elaphomyces* species, identified according to our own experience based on abundant fresh material as well as on revision of herbarium collections from the museums of Torino (TO), Kew (K(M)), Łódź (LOD), Paris (PC) and Uppsala (UPS), including original material from Vittadini and the Tulasne brothers.

Vittadini's material is responsible for an issue in the taxonomy of hypogeous fungi, as this generous author liberally sent to many of his correspondents undated samples of his species (Lloyd 1923: 1222). Despite the efforts of O. Mattiolo to gather in the Torino herbarium most of Vittadini's authentic collections spread over private herbaria and museums worldwide, it appears impossible to consider any of these collections, in TO as well as in PC (especially Montagne's and the Tulasnes'

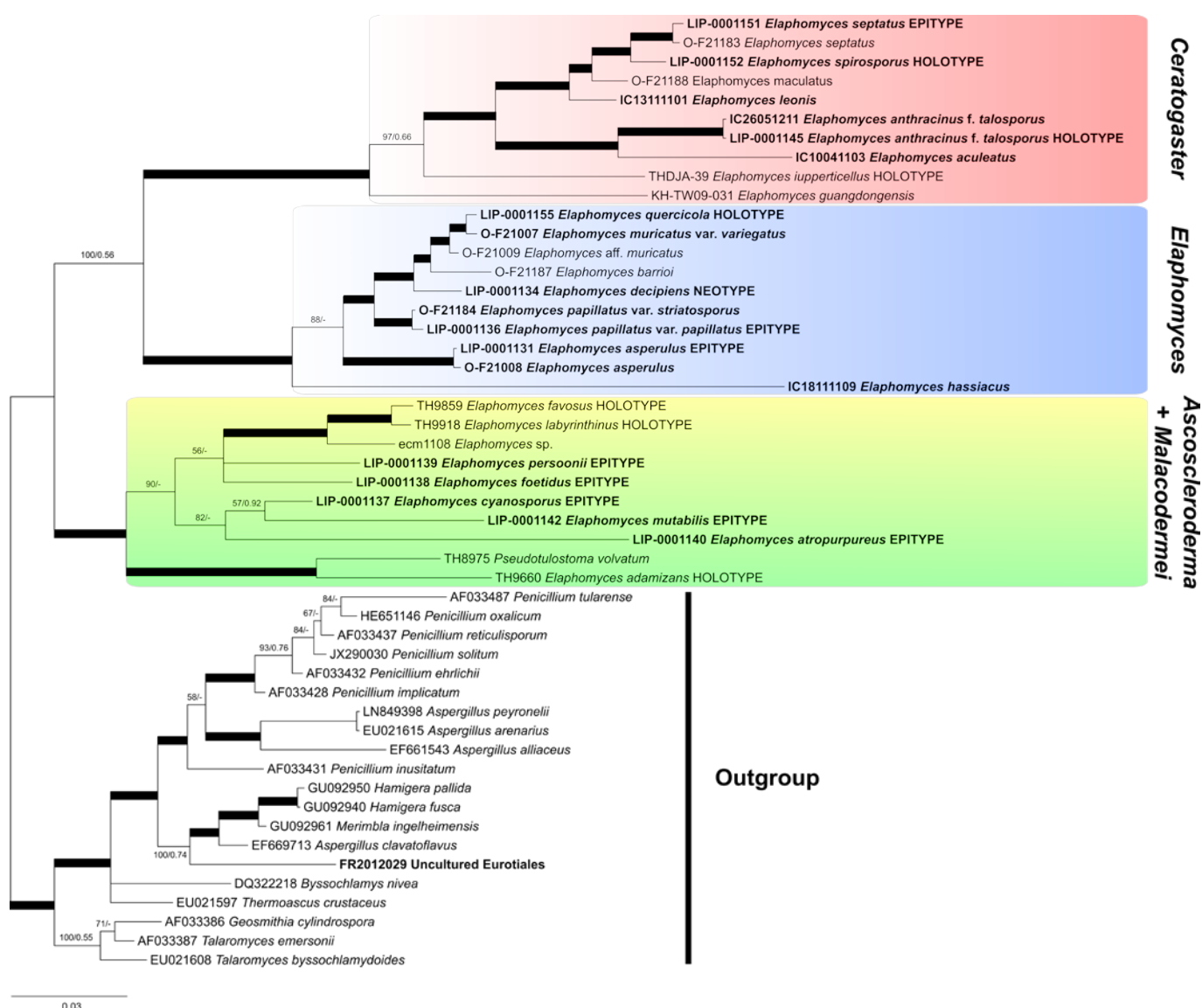


Fig. 1 Phylogeny of European *Elaphomyces*, inferred from a combined phylogenetic analysis of nuclear rDNA sequences. Fifty percent majority rule Bayesian consensus tree of a representative set of European *Elaphomyces* (ITS + 28S) sequences. Thick branches are supported by Posterior Probability (BPP) $\geq 95\%$ and SH-aLRT ≥ 0.8 (Materials and Methods). Numbers by nodes indicate Bayesian and ML support for branches that do not meet this level of credibility. Colour boxes indicate Sections.

collections), K(M) (Berkeley's collections) and UPS (Fries' collections) as original material eligible as lectotypes (as discussed by Vizzini et al. 2010, with an exception for *E. foetidus*; see Paz et al. 2012 and below). Dodge (1929) also cited a few 'authentic' collections from Vittadini in Patouillard's herbarium (FH), and more parts exist in various European and American herbaria (Stafleu & Cowan 1986: 760). When no material could be proved as original, Vittadini's illustrations are designated as lectotypes; other nomenclatural aspects are detailed in the taxonomic conspectus presented below.

MATERIALS AND METHODS

Sampling and morphological analyses

Ascomata cited as 'Material studied' below were collected by the authors or their correspondents, with or without help of trained dogs, mainly in Norway and Spain, with additional collections from France, Greece, Italy and Sweden. Morphological descriptions were made on fresh material and completed on exsiccata when opportune. Macro photographs were made with a Nikon D7100 body with self-made magnifying objectives by C. Lavoise. Microscopical observations and pictures were made on a trinocular microscope Nikon Eclipse E800,

coupled with a Nikon D5000 or D7100 camera body, pictures were acquired with the software 'Helicon remote' and treated and assembled with the software 'Helicon focus'. Material for microscopical observations was mounted in water or Hoyer's medium. Collections are deposited in the herbaria GB (University of Gothenburg, Sweden), LIP (Faculté des sciences pharmaceutiques et biologiques, Université Lille 2, France), O (University of Oslo, Norway) and LOD (Łódź University, Poland), with duplicates in A. Paz' personal herbarium (as 'IC' below) and in other fungal collections abbreviated as follows: CEFE (CEFE-CNRS, Montpellier, France), ERD (E. Rubio's personal herbarium), JMV (J.M. Vidal's personal herbarium) and PCH (P. Chautrand's personal herbarium).

Historical collections were observed and photographed, with minute samples of gleba and peridium (cross-sections) sampled and provisionally mounted on glass slides during visits of the authors in the herbaria K(M) (Kew, United Kingdom), PC (Paris, France) and TO (Torino, Italy), with authorisation of the curators. For observations, the samples were mounted as described previously in Hoyer's medium. Remaining material is kept in A. Paz' personal collections. Most ascospores observed from original or authentic material are illustrated in Fig. 4 and indicated as such in the following lists of 'material studied'.

Fig. 2a

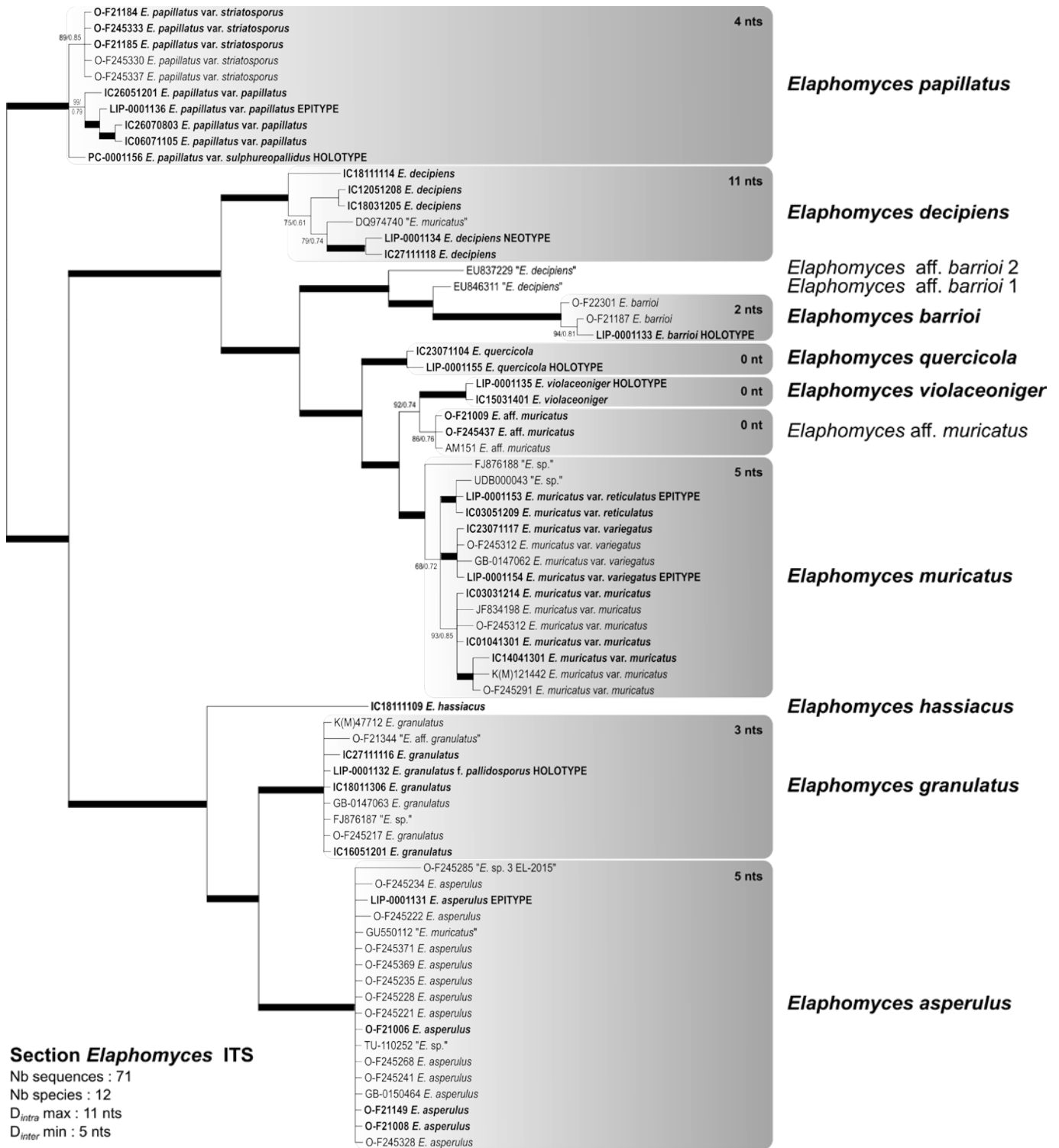


Fig. 2 Phylogenetic organization and species limits of European *Elaphomyces*, inferred from combined phylogenetic analyses of ITS sequences. Fifty percent majority rule Bayesian consensus tree of European *Elaphomyces* ITS sequences. Thick branches are supported by Posterior Probability (BPP) $\geq 95\%$ and SH-aLRT ≥ 0.8 (Materials and Methods). Numbers by nodes indicate Bayesian and ML support for branches that do not meet this level of credibility. When two sequences or more are available, grey boxes delimit accepted species and the maximal intraspecific genetic distance (D_{intra} max) of each of them is assessed as absolute number of nucleotide differences, excluding gaps (Materials and Methods). Species described in the present work are named in **bold**. Main phylogenetic features for each section are summarized by the side of each phylogram. a = section *Elaphomyces*; b = section *Ceratogaster*; c = sections *Ascoscleroderma* (yellow dotted box) + *Malacodermei* (green dotted box)

Fig. 2b

Section *Ceratogaster* ITS

Nb sequences : 34

Nb species : 10

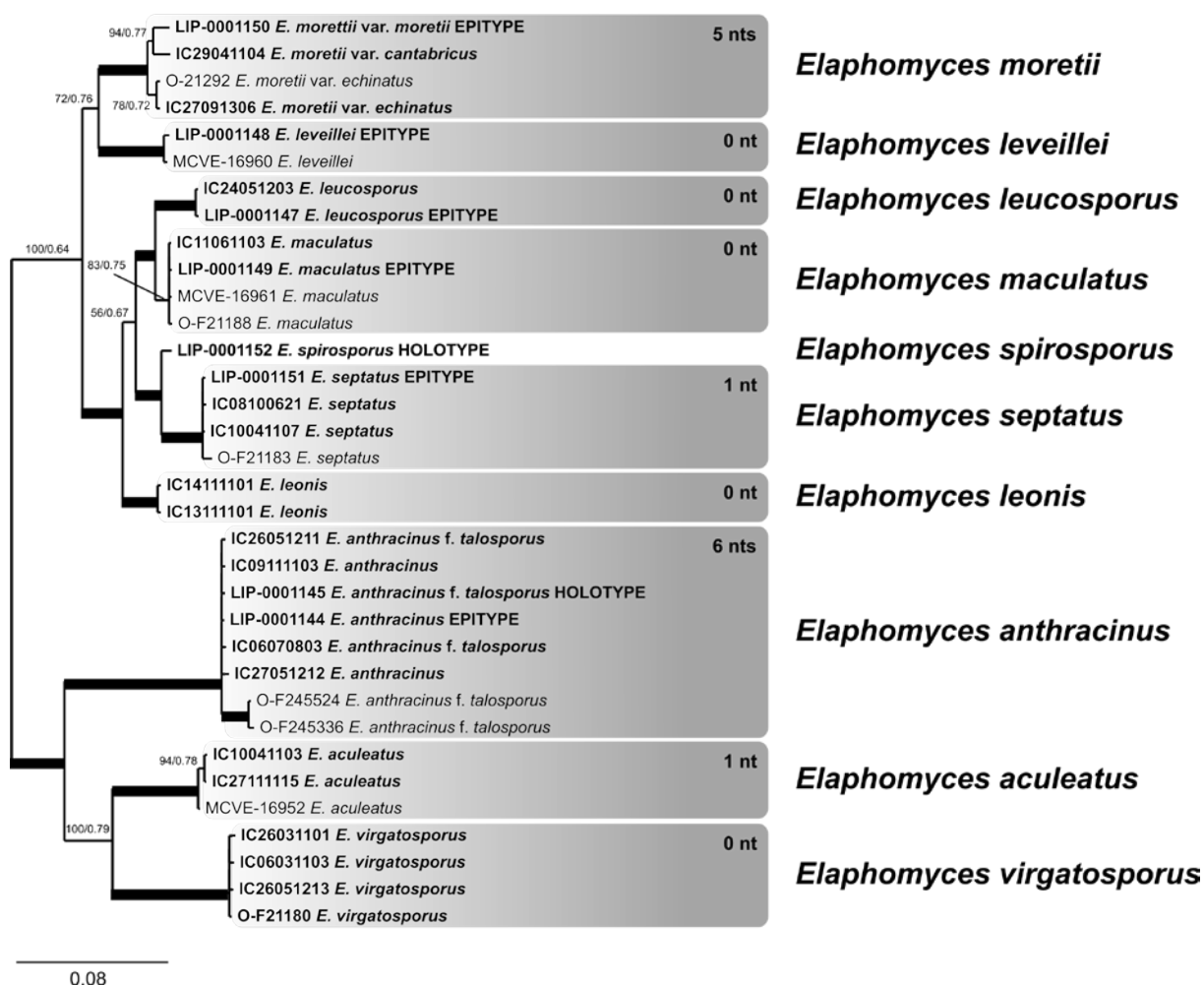
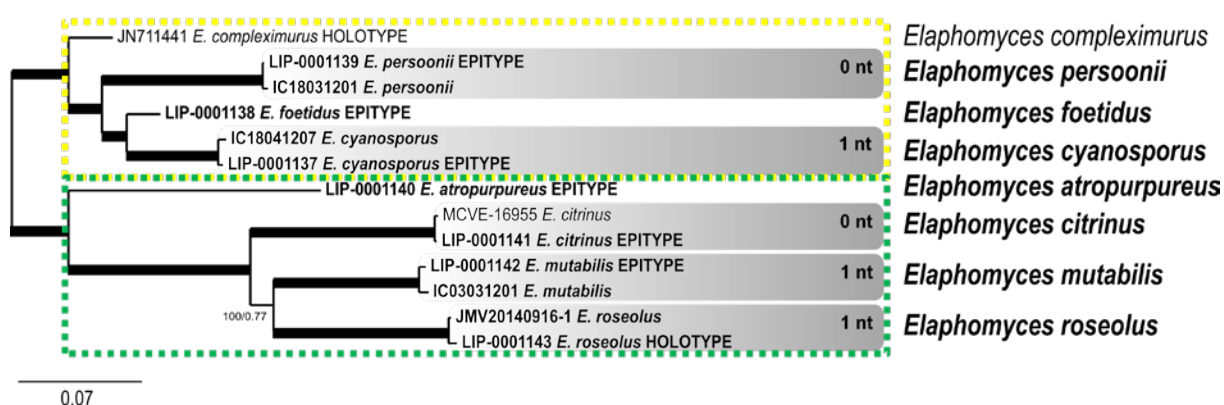
*D*_{intra} max : 6 nts*D*_{inter} min : 10 nts

Fig. 2c

Sections *Ascocladerma* + *Malacodermei* ITS

Nb sequences : 13

Nb species : 8

*D*_{intra} max : 1 nt*D*_{inter} min : 23 nts

DNA extraction and sequencing

Eighty-one specimens of *Elaphomyces* from a broad geographic distribution in Europe were targeted for sequencing in this study. Sequences from the complete ITS region and about 1200 base pairs of the 5' end of the 28S nuclear ribosomal DNA were generated. DNA extraction and PCR were performed using REExtract-N-Amp[™] Plant PCR Kit (Sigma-Aldrich, St. Louis, MO, USA) and as previously described in Larsson & Örstadius (2008) and Richard et al. (2015). Primers used to amplify the ITS were ITS1F-ITS4 (Gardes & Bruns 1993) or ITS1F-LR21, the 28S with LR0R-LR7 (Hopple & Vilgalys 1999). Primers used for sequencing were ITS1, ITS4 (White et al. 1990), LR0R, LR7 or LR5 (Hopple & Vilgalys 1999) and Ctb6 <https://nature.berkeley.edu/brunslab>. Sequencing of both strands was done at Eurofins Genomics (Ebersberg, Germany) or Macrogen (Korea).

Sequences were edited and assembled using Codon Code Aligner v. 4.1.1 (CodonCode Corp., Centerville, MA, USA) or Sequencher v. 5.1 (Gene Codes, Ann Arbor, Michigan). Generated sequences have been deposited in GenBank. Sequenced specimens are indicated by * in the list of material studied, and with the accession numbers in **bold** in Table 1.

Datasets and phylogenetic analyses

Four sequence datasets were assembled and separately analysed. Dataset 1 (analysed in Fig. 1) includes ITS + 28S concatenated sequences of 22 European collections of *Elaphomyces*, seven published sequences of *Elaphomyces* or *Pseudotulostoma*, and 20 sequences of Eurotiales as outgroup. Datasets 2–4 (analysed in Fig. 2) include ITS sequences of mostly European collections that belong in, respectively, sect. *Elaphomyces*, sect. *Ceratogaster* and sect. [*Malacodermei* + *Ascoscleroderma*], including 44 sequences published and accessed from GenBank (www.ncbi.nlm.nih.gov/genbank) and UNITE (Kõljalg et al. 2013) databases, and 73 sequences gen-

erated for this study, deposited in GenBank and (for collections from Norway and Sweden) in the BOLD (www.boldsystems.org) database. Phylogenetic analyses were all performed online at <http://phylogeny.lirmm.fr/> (Dereeper et al. 2008) and on the CIPRES Science Gateway (www.phylo.org/index.php/). Multiple sequence alignment was carried out with MUSCLE v. 3.7 (Edgar 2004). Alignments were edited with Gblocks 0.91b, with defaults settings for Dataset 1 and set to lowest stringency in the selection of conserved blocks for Datasets 2–4 (Castresana 2000, Talavera & Castresana 2007). Maximum likelihood (ML) phylogenetic analyses were performed with PhyML v. 3.0 (Guindon et al. 2010), using the GTR + I + Γ model of evolution and the Shimodaira-Hasegawa version of the approximate likelihood-ratio test (SH-aLRT) of branch support, that displays accuracy comparable to 70 % standard bootstrapping when > 0.8 (Anisimova et al. 2011, Bellanger et al. 2015). Bayesian inference of phylogeny was assessed using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003). Sixteen Markov Chain Monte Carlo (MCMC) were performed in four separate runs of 1 000 000 generations, with stationarity convergence estimated by the Potential Scale Reduction Factor = 1 (Gelman & Rubin 1992). Trees and parameters were sampled every 1 000 generations (1 000 trees), with an initial burn-in set to 25 % (250 trees). A 50 % majority-rule consensus phylogram was computed from the remaining trees; the proportions of this tree correspond to Bayesian posterior probabilities (BPP), that are considered as significant when ≥ 95 %. Trees were built using TreeDyn 198.3 (Chevenet et al. 2006) or FigTree 1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree/>) and edited with Inkscape 0.91 (<https://inkscape.org/fr/>).

Species limits and ITS barcoding

Species accepted in the present work are strictly phylogenetic, i.e. they correspond to terminal sister-clades in the ITS phylogram, that display reciprocal monophyly and significant branch

Table 2 Intraspecific variability and phylogenetic borders of European *Elaphomyces* species.

Section	Species	D intra max ¹	D inter min to E. closest species ¹	Genus-wide ITS barcoding ²
<i>Elaphomyces</i>	<i>E. asperulus</i>	5 nts	18 nts to <i>E. granulatus</i>	Yes
	<i>E. barrioi</i>	2 nts	13 nts to <i>E. aff. barrioi</i> 1	Yes
	<i>E. aff. barrioi</i> 1	na	10 nts to <i>E. aff. barrioi</i> 2	na
	<i>E. aff. barrioi</i> 2	na	10 nts to <i>E. aff. barrioi</i> 1	na
	<i>E. decipiens</i>	11 nts	22 nts to <i>E. aff. muricatus</i>	Yes
	<i>E. granulatus</i>	3 nts	18 nts to <i>E. asperulus</i>	Yes
	<i>E. hassiacus</i>	na	26 nts to <i>E. granulatus</i>	na
	<i>E. muricatus</i>	5 nts	9 nts to <i>E. aff. muricatus</i>	No
	<i>E. aff. muricatus</i>	0 nt	9 nts to <i>E. muricatus</i>	No
	<i>E. papillatus</i>	4 nts	37 nts to <i>E. granulatus</i>	Yes
	<i>E. quercicola</i>	0 nt	10 nts to <i>E. aff. muricatus</i>	No
	<i>E. violaceoniger</i>	0 nt	5 nts to <i>E. aff. muricatus</i>	No
<i>Ascoscleroderma</i>	<i>E. compleximurus</i>	na	23 nts to <i>E. foetidus</i>	na
	<i>E. cyanosporus</i>	1 nt	24 nts to <i>E. foetidus</i>	Yes
	<i>E. foetidus</i>	na	24 nts to <i>E. cyanosporus</i>	na
	<i>E. persoonii</i>	0 nt	29 nts to <i>E. foetidus</i>	Yes
<i>Malacodermei</i>	<i>E. atropurpureus</i>	na	68 nts to <i>E. compleximurus</i>	na
	<i>E. citrinus</i>	0 nt	48 nts to <i>E. mutabilis</i>	Yes
	<i>E. mutabilis</i>	1 nt	48 nts to <i>E. citrinus</i>	Yes
	<i>E. roseolus</i>	1 nt	52 nts to <i>E. mutabilis</i>	Yes
<i>Sclerodermei</i>	<i>E. aculeatus</i>	1 nt	43 nts to <i>E. virgatosporus</i>	Yes
	<i>E. anthracinus</i>	6 nts	57 nts to <i>E. aculeatus</i>	Yes
	<i>E. leonis</i>	0 nt	14 nts to <i>E. spirosporus</i>	Yes
	<i>E. leucosporus</i>	0 nt	10 nts to <i>E. maculatus</i>	No
	<i>E. leveillei</i>	0 nt	24 nts to <i>E. moretii</i>	Yes
	<i>E. maculatus</i>	0 nt	10 nts to <i>E. leucosporus</i>	No
	<i>E. moretii</i>	5 nts	24 nts to <i>E. leveillei</i>	Yes
	<i>E. septatus</i>	1 nt	12 nts to <i>E. spirosporus</i>	Yes
	<i>E. spirosporus</i>	na	12 nts to <i>E. septatus</i>	na
	<i>E. virgatosporus</i>	0 nt	43 nts to <i>E. aculeatus</i>	Yes

¹ Maximal intraspecific (D intra max) and minimal interspecific (D inter min) phylogenetic distances are expressed as absolute nucleotide (nts) differences, excluding gaps. na = not applicable (single sequence).

² Barcoding is set to yes when D intra max < 11.6 nts (genus-wide barcode gap, cf. Fig. 3) < D inter min. na = not applicable (no D intra max).

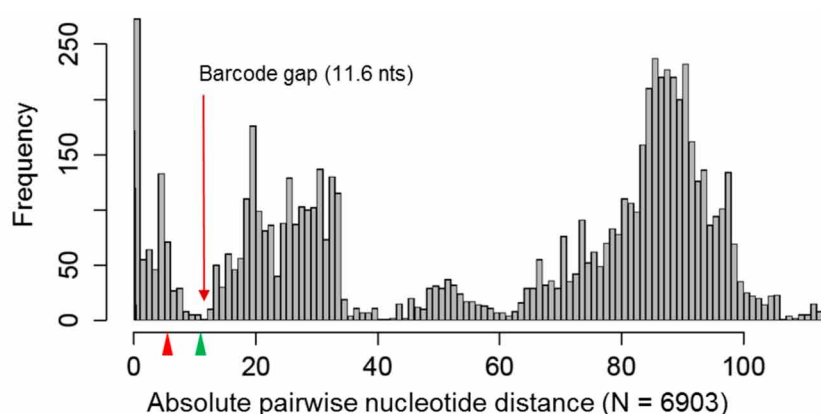


Fig. 3 Frequency of distribution of absolute pairwise phylogenetic distances within *Elaphomyces* ITS sequences. The barcode gap of the genus, defined as the shortest minimal frequency of distribution (Materials and Methods), corresponds to 11.6 nucleotide differences, as indicated by the red arrow. The maximal intraspecific phylogenetic distance ($D_{intra\ max}$) and the minimal interspecific phylogenetic distance ($D_{inter\ min}$) of species accepted in the present study, are marked by green and red arrowheads, respectively. Note that, at the genus level, $D_{intra\ max} > D_{inter\ min}$, indicating that not all *Elaphomyces* species, as defined here, can be resolved by an ITS barcoding approach.

support ($BPP \geq 95\%$ and $SH-aLRT > 0.8$). This definition is intended to identify the smallest possible phylogenetic units that share common evolutionary history. Maximal intraspecific phylogenetic distance ($D_{intra\ max}$) and minimal interspecific phylogenetic distance ($D_{inter\ min}$) were associated with each species and expressed as absolute number of nucleotide differences, excluding gaps (Table 2). The compatibility of the identified species with an ITS barcoding recognition method was assessed by a $D_{inter\ min}/D_{intra\ max}$ ratio > 1 . To estimate the barcode gap value at the genus scale, we plotted the 6 670 ($N(N-1)/2$, with $N = 116$) pairwise phylogenetic distances as a function of their frequency across the whole ITS dataset (Fig. 3), using R software (R Core team 2012). The barcode gap within *Elaphomyces* was then identified as the first minimum of the function of distribution of pairwise distances (Frøslev et al. 2007, Schoch et al. 2012, Osmundson et al. 2013, Bellanger et al. 2015).

Intraspecific taxa were assigned the varietal rank when supported by both ITS phylogeny and morpho-anatomy. Forms were defined as ‘distinct phenotypes of no persistent populational significance’, following Cronquist (1988) and Hamilton & Reichard (1992), when collections showing noticeable morpho-anatomical singularities do not form monophyletic lineages among typical collections.

RESULTS

DNA phylogeny

Based on current sampling, *Elaphomyces* encompasses three lineages, strongly supported as monophyletic by both ML and Bayesian phylogenetic analyses of (ITS + 28S) rDNA sequences (Fig. 1). Two of these lineages correspond to sections *Elaphomyces* and *Ceratogaster* and are therefore also supported by consistent morphological diagnostic features. The third, basal lineage encompasses the two sections *Ascoscleroderma* and *Malacodermei*, together with the genus *Pseudotulostoma*, but neither the internal topology of the clade nor branch supports do further resolve the limits of these taxa within *Elaphomyces* (Fig. 1). Considering the high diversity of species described by Castellano et al. (2011, 2012a) from the Southern Hemisphere and morphologically attributable to sect. *Malacodermei*, a European-based classification most likely will not reflect the evolutionary history of this Gondwanian genus. Phylogenetic analyses of more southern species of *Elaphomyces* will be necessary to better delineate the evolutionary

boundaries of these basal groups. For the purpose of this paper, sections *Ascoscleroderma* and *Malacodermei* are provisionally maintained in their historical, morpho-anatomic definition.

As defined here, *Elaphomyces* species are primarily phylogenetic units, supported by both the tree topology and branch support values (Materials and Methods). In addition, each of them displays intraspecific ITS variability lower than the minimal phylogenetic distance separating it from its closest relative ($D_{intra\ max} < D_{inter\ min}$), making them prone to ITS DNA barcoding. To ascertain how many of them would be identified by a genus-wide ITS barcoding approach of species limits finding, we computed the barcode gap value (BC) from the distribution frequency of pairwise phylogenetic distances of our ITS dataset, and found that it represents 11.6 nucleotide differences (Fig. 3). The highest $D_{intra\ max}$ (11 nts, green arrowhead in Fig. 3) of our dataset exceeds the shortest $D_{inter\ min}$ (9 nts, red arrowhead in Fig. 3), indicating that no phylogenetic distance can theoretically satisfy the barcode gap criterion of species limits delineation: $D_{intra\ max} < BC < D_{inter\ min}$. Using the 11.6 nts gap as a threshold would filter out five species that nonetheless fulfil our phylogenetic criteria: *E. aff. barrioi* 1 / *E. aff. barrioi* 2, *E. aff. muricatus* / *E. quercicola* / *E. violaceoniger*, and *E. leucosporus* / *E. maculatus* (Table 2). Thus, 83 % (25/30) of *Elaphomyces* species defined in the present work can be identified by genus-wide ITS barcoding.

Taxonomy

***Elaphomyces* Nees:** Fr. in Nees von Esenbeck & Nees von Esenbeck, *Gesch. merkw. Pilze* 4: LXIX. 1820

Holotype. *Lycoperdon cervinum* L. (Nees von Esenbeck & Nees von Esenbeck 1820: LXIX, as ‘*Scleroderma cervinum* Pers.’; see Dodge 1929: 157).

Synonyms. *Hypogaeum* Pers., Roemer Neues Mag. Bot. 1: 87. 1794. *Holotype:* *Lycoperdon cervinum* L. = *E. granulatus*.

Elaphomyces subsect. *Hypogaeum* (Pers.) C.W. Dodge, *Ann. Mycol.* 27 (3–4): 159. 1929.

Phymatium Chevall., *Fl. Gen. Env. Paris* 1: 361. 1826. *Holotype:* *Phymatium fulvum* Chevall. (Chevallier 1826) = *E. granulatus*.

Ceraunium Theophr. ex Wallr., *Fl. Crypt. Germ.* 2: 405. 1833. *Holotype:* *Elaphomyces granulatus* (Alb. & Schwein.: Fr.) Fr. (Wallroth 1833).

Elaphomyces sect. *Ceraunium* (‘*Ceraunion*’) (Theophr. ex Wallr.) Fr., *Summa Veg. Scand.* 2: 445. 1849.

Ceratogaster Corda, *Deutschl. Fl. III*, 19–20: 35. 1841. *Holotype:* *Elaphomyces maculatus* Vittad. (Corda 1841: 35).

Elaphomyces sect. *Ceratogaster* (Corda) Fr., *Summa Veg. Scand.* 2: 445. 1849.



Fig. 4 Ascospores of *Elaphomyces* spp. 1. *E. asperulus* (TO, Vittadini); 2. *E. granulatus* forma *granulatus* (Mougeot & Nestler 1812 n° 282, LIP); 3. *E. granulatus* forma *pallidosporus* (holotype); 4. *E. hassiacus* (IC18111109); 5. *E. barrioi* (holotype); 6. *E. decipiens* (neotype); 7. *E. muricatus* var. *muricatus* (PC, Vittadini); 8. *E. muricatus* var. *reticulatus* (epitype); 9. *E. muricatus* var. *variegatus* (PC, Vittadini); 10. *E. quercicola* (LOD 20335); 11. *E. violaceoniger* (holotype); 12. *E. papillatus* var. *papillatus* (TO, Vittadini); 13. *E. papillatus* var. *striatosporus* (O-F21185); 14. *E. papillatus* var. *sulphureopallidus* (holotype); 15. *E. cyanosporus* (lectotype); 16. *E. foetidus* (lectotype); 17. *E. persoonii* (PC, Vittadini); 18. *E. atropurpureus* (PC, Vittadini); 19. *E. citrinus* (PC, Vittadini); 20. *E. mutabilis* (PC, Vittadini); 21. *E. roseolus* (holotype); 22. *E. aculeatus* (TO, Vittadini); 23. *E. anthracinus* forma *anthracinus* (PC, Vittadini); 24. *E. anthracinus* forma *talosporus* (holotype); 25. *E. virgatosporus* (IC26051213); 26. *E. leonis* (holotype); 27. *E. leucosporus* (TO, Vittadini); 28. *E. leveillei* (lectotype); 29. *E. maculatus* (PC, Vittadini); 30. *E. moretii* var. *moretii* (TO, Vittadini); 31. *E. moretii* var. *cantabricus* (IC29041104); 32. *E. moretii* var. *echinatus* (PC, Vittadini); 33. *E. septatus* (TO, Vittadini); 34. *E. spirosporus* (holotype). — Scale bar = 10 µm. — Photos: A. Paz.

Lycoperdastrum Haller ex Kuntze, Revis. Gen. Pl. 2: 858. 1891. Holotype: *Lycoperdon cervinum* L. = *E. granulatus*.

Ascoscleroderma Clémencet, Botaniste 24: 14. 1932. Holotype: *Elaphomyces cyanosporus* Tul. & C. Tul.

?*Pseudotulostoma* O.K. Mill. & T.W. Henkel in Miller et al., Mycol. Res. 105, 10: 1269. 2001. Holotype: *Pseudotulostoma volvatum* ('*volvata*') O.K. Mill. & T.W. Henkel (after Reynolds 2011, Castellano et al. 2012c, 2016).

Elaphomyces sect. *Elaphomyces*

Synonym. *Elaphomyces* sect. *Ceraunium* (Theophr. ex Wallr.) Fr., Summa Veg. Scand. 2: 445. 1849.

Notes — As established by Fontana (1909) and phylogenetically supported here, this section splits into two main lineages that are here formally given the subsection rank: the *E. granulatus*-group ('sottogruppo *E. granulatus*', with non-marbled inner peridium), as subsect. *Elaphomyces*, and the *E. muricatus*-group ('sottogruppo *E. variegatus*', with marbled inner peridium), as subsect. *Muricati*. *Elaphomyces papillatus*, with differently ornamented spores, emerges as a third, monospecific lineage here referred to as subsect. *Papillati* (Fig. 1, 2a).

Elaphomyces subsect. *Elaphomyces*

Elaphomyces asperulus Vittad., Monogr. Tuberacearum: 69. 1831 — Fig. 4.1, 5a–b

Synonyms. *Lycoperdastrum asperulum* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Elaphomyces cervinus var. *asperulus* (Vittad.) E. Fisch., Rabenh. Krypt.-Fl., ed. 2, 1, 5: 96. 1897.

Lectotype (here designated MBT374412): iconotype, Vittadini 1831, Monogr. Tuberacearum, pl. IV, f. 6 (only certified original material).

Epitype (here designated MBT374413): SPAIN, Asturias, San Esteban de Cuñaba, under *Castanea sativa*, 13 May 2012, A. Paz & C. Lavoise (LIP 0001131); isoeotype in herb. pers. A. Paz (IC13051208)*.

Elaphomyces granulatus b. [unranked] *costatolacunosus* ('*costato-lacunosum*') Fr.: Fr. in Fries, Syst. Mycol. III: 38. 1829 (based on *Elaphomyces granulatus* ss. Hornemann 1829, *Flora Danica* pl. 1969, f. 1).

Elaphomyces rugosus Fr., Summa Veg. Scand. 2: 445. 1849 (*nomen novum* based on *Elaphomyces granulatus* b. [unranked] *costatolacunosus* Fr., Syst. Mycol. III: 38. 1829).

Elaphomyces asperulus var. *rugosus* (Fr.) C.W. Dodge, Ann. Mycol. 27, 3–4: 178. 1829.

Elaphomyces asperulus forma *microsporus* Fontana, Mem. Accad. Sci. Torino II, 59: 104. 1909.

Additional material studied. FRANCE, Savoie, Mâcot-la-Plagne, forêt domaniale, under *Picea abies* and *Larix decidua*, 25 Aug. 1988, M. Meyer (IC25088803). — HUNGARY, Kecskemét, Brassó, pine forest, 10 July 1839, L. Hollós (TO, coll. O. Mattiolo, as '*E. variegatus*'). — ITALY, Trentino Selva di Fiano, val di Fiemme, within roots of *Picea abies*, Aug. 1897, G. Bresadola (TO, as '*E. cervinum* b. *asperulus* Vitt.') (Fig. 4.1); s.loc., s.d., C. Vittadini (TO, authentic material of *E. asperulus*); ibid., (PC, herb. C. Montagne CM4379, authentic material of *E. asperulus*); ibid., C. Vittadini, comm. M.J. Berkeley (PC, herb. C. Montagne 4380); Bergamo, Dossena, Vaccareggiozona, Cascina Vecchia, *Picea Abies* and *Fagus sylvatica*, 8 July 2009, A. De Vito (IC8070931); ibid., 20 Sept. 2011, A. De Vito (IC20091128); ibid., 10 Nov. 2013, A. De Vito (IC10111323). — NORWAY, Nord-Trøndelag, Steinkjer, Nedre Skratåsén, in mossy, semirich *Picea* forest, 17 Oct. 2011, A. Molia & L. Hund (O-F21008); Steinkjer, Stod, *Picea* forest on carbonated soil, 19 Oct. 2011, A. Molia & L. Hund (O-F21149); Akershus, Asker, Nesøya, close to Nesøytjern, in mossy, swampy *Picea* forest on carbonated soil, 13 Nov. 2011, A. Molia, K. Killingmo, K. Hund & L. Hund (O-F21006); Ullensaker, N of Hofmoen (Ø of Gardermoen Airport), in mossy *Picea* forest, 18 Mar. 2012, A. Molia & L. Hund (O-F245228)*; Østfold, Hvaler, Asmaløy, Skipstadsand, under *Corylus avellana*, 6 Oct. 2012, T. Læssøe (O-F245371)*; ibid., in sandy soil under *Quercus*, 6 Oct. 2012, K.M.W. Sæbø (O-F245369)*; Buskerud, Flesberg, Molia, in mossy *Picea* forest, 26 Mar. 2012, A. Molia & L. Hund (O-F245235)*; ibid., 27 Mar. 2012 (O-F245241)*; Ringerike, Viksåsén, in mixed *Pinus* & *Corylus* forest on carbonated soil, 2 Aug. 2012, A. Molia & L. Hund (O-F245268)*; Hole, Burudåsen, in mixed *Pinus* & *Corylus* forest on carbonated soil, 18 Sept. 2012, A. Molia & L. Hund,

(O-F245328)*; Hedmark, Ringsaker, Moelv, in mossy mixed *Pinus* & *Picea* forest, 15 Mar. 2012, A. Molia & L. Hund, (O-F245221)*; ibid., 15 Mar. 2012, A. Molia & L. Hund, (O-F245222)*; Østfold, Skjeberg, in mossy *Picea abies* forest, 25 Mar. 2012, A. Molia & L. Hund (O-F245234); Nord-Trøndelag, Grong, in mossy *Picea abies* forest with *Vaccinium myrtillus*, T. Læssøe & A. Molia (O-F245285)*; Steinkjer, Skratåsén, Nedre, in *Picea abies* forest on semi-rich soil, 17 Oct. 2011, A. Molia & L. Hund (AM40, O-F21008)*; O- and Steinkjer, Stod, in calcareous *Picea abies* forest, 19 Oct. 2011, A. Molia & L. Hund (AM44, O-F21149)*. — SPAIN, Asturias, Cuñaba, under *Corylus avellana*, *Fagus sylvatica* and *Quercus robur*, 6 June 2010, A. Paz (IC06061027); ibid., 4 Apr. 2011, A. Paz (IC04041127); 23 Apr. 2014, A. Paz & C. Lavoise (IC23051401); Cádiz, Los Barrios, Monte Mojea Conejo, Carril de los Garlitos, *Quercus canariensis* and *Quercus suber*, 29 Nov. 2015, A. Paz & C. Lavoise (IC29111502); Cantabria, Bielsa, under *Quercus rubra* and *Fagus sylvatica*, 28 June 2008, A. Paz (IC28060829); Cambillas, Saja, under *Corylus avellana* and *Fagus sylvatica*, 3 July 2008, A. Paz (IC03070831); Girona, Camprodon, Setcases-Baga de Carboner, under *Abies alba*, 20 Oct. 1997, J.-M. Vidal, (JMV970920–1); Málaga, Cortes de la Frontera, La Calderona, *Quercus faginea* and *Quercus suber*, 24 Nov. 2015, A. Paz & C. Lavoise (24111504); El Palancar, under *Quercus faginea* and *Quercus suber*, 28 Nov. 2015, A. Paz & C. Lavoise (IC28111503). — SWEDEN, Småland, Femsjö, under *Pinus sylvestris*, *Quercus robur*, *Picea abies* and *Fagus sylvatica*, 14 Mar. 2014, A. Molia & L. Hund (AM35-2014, GB-0150464)*; ibid., under *Betula pendula*, *Pinus sylvestris* and *Fagus sylvatica*, 16 Mar. 2014, A. Molia & L. Hund (AM43-2014, GB-0147062).

Notes — This is one of the most common and widespread species in Europe, well-characterised by its purplish tinged peridium (Fischer 1897a: 96) and ascospores ornamented by patches of confluent warts. Some specimens with a spectacular blue halo in the outer layer of the peridium have been observed without and within typical collections of *E. asperulus*, in Norway (O-F245221, O-F245241, O-F245268 and O-F245328) and Spain (JMV970920–1). A bluish tinged peridium is also observed in *E. hassiacus* (see below).

The relatively high ITS polymorphism of *E. asperulus* (5 nts, Table 2) is driven by O-F245285, a single Norwegian collection that lacks noticeable morpho-anatomic differences when compared to other European specimens examined. More extensive sampling of the clade will be necessary to support a putative infraspecific taxon within this species. Phylogenetically, the closest relative to *E. asperulus* is *E. granulatus* but the two species are well separated, as assessed by a D inter min/D intra max ratio > 3 (Table 2).

Elaphomyces granulatus (Alb. & Schwein.: Fr.) Fr. **forma granulatus** in Fries Syst. Mycol. 3: 58. 1829 — Fig. 4.2, 5c–e

Basionym. *Scleroderma cervinum* α [unranked] *granulatum* Alb. & Schwein.: Fr., Consp. Fungorum Lusat.: 81. 1805.

Synonyms. *Elaphomyces vulgaris* β [unranked] *granulatus* (Alb. & Schwein.: Fr.) Corda, Deutschl. Fl., III, 19–20: 25. 1841.

Lycoperdon cervinum L., Sp. Pl. 2: 1183. 1753.

Boletus cervinus (L.) Valmont, Dict. Rais. Hist. Nat. 3e ed., 1: 506. 1775 (not *B. cervinus* Schwein.: Fr. = *Trametopsis cervina*).

Hypogaeum cervinum (L.) Pers., Tent. Disp. Meth. Fung.: 7. 1797.

Scleroderma cervinum (L.) Pers., Syn. Meth. Fung.: 156. 1801.

Elaphomyces cervinus (L.) Schldt., Fl. Berol. 2: 166. 1824.

Lycoperdastrum cervinum (L.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lycoperdon solidum L. ex Sm., Fl. Lapp. ed. alt.: 386. 1792.

Phymatium fulvum Chevall., Fl. Gén. Env. Paris 1: 361. 1826.

Elaphomyces officinalis Nees, Pl. Off. 16: 12. 1827.

Elaphomyces leucocarpus Vittad., Monogr. Tuberacearum: 72. 1831.

Elaphomyces vulgaris δ [unranked] *columellifer* Corda in Sturm, Deutschl. Fl. III, 19–20: 31. 1841 (cited as '*E. vulgaris* δ *columellifer* Corda' by Saccardo 1889: 868).

Elaphomyces plicatus R. Hesse, Hypog. Deutschl. 2: 74. 1894.

Elaphomyces cervinus var. *plicatus* (R. Hesse) E. Fisch., Rabenh. Krypt.-Fl., ed. 2, 1, 5: 96. 1897.

(for pre-Linnean synonyms, see Fries 1909).

Material studied. FRANCE, Vosges, s.loc., 1912, Mougeot & Nestler's *Stirp. Cryptog. Voges.-Rhen.* n° 282, original material of *E. granulatus*



Fig. 5 a–b. *Elaphomyces asperulus*. a. Ascospores (TO, Vittadini); b. ascomata (LIP 0001131, epitype). — c–e. *Elaphomyces granulatus* forma *granulatus*. c. Ascomata (Mougeot & Nestler 1812 n° 282, LIP); d. ascomata (IC18011306); e. ascospores (Mougeot & Nestler 1812 n° 282, LIP). — f–i. *Elaphomyces granulatus* forma *pallidosporus* (IC21071103, holotype). f, h. Ascomata; g. ascospores; i. details of the peridium. — Scale bars: a, e, g = 10 µm; b–d, f, h = 1 cm; i = 1 mm. — Photos: a, e, g, i. A. Paz; b–d. C. Lavoise; f, h. De Vito.

(LIP) (Fig. 4.2); *ibid.* (UPS). — ITALY (?), s.loc., s.d., *C. Vittadini*, transmitted by M.J. Berkeley (PC, herb. C. Montagne CM4389, as '*E. leucocarpus*', authentic material). — NORWAY, Østfold, Hvaler, 25 Feb. 2012, under *Picea*, *Quercus* and *Pinus*, L. Hund, A. Molia & R. Kristiansen (O-F245217)*. — PORTUGAL, Figueira de Castelo Rodrigo, *Quercus ilex* and *Juniperus oxycedrus*, 9 Nov. 2015, A. Paz & C. Lavoise (IC09111503). — SPAIN, Asturias, Cuñaba, *Castanea sativa* and *Fagus sylvatica*, 11 Nov. 2013, A. Paz & C. Lavoise (IC11111304); Asturias, San Esteban de Cuñaba, *Castanea sativa*, 27 Nov. 2011, A. Paz & C. Lavoise (IC27111116)*; Cádiz, Los Barrios, Monte Mojea Conejo, Carril de los Garlitos, *Quercus canariensis* and *Quercus suber*, 29 Nov. 2015, A. Paz & C. Lavoise (IC29111501); El Cuartón, Bosque de Niebla, *Quercus canariensis*, *Quercus pyrenaica* and *Quercus suber*, 25 Nov. 2015, A. Paz & C. Lavoise (IC25111502); *ibid.*, 1 Dec. 2015, A. Paz & C. Lavoise (IC01121511); Cantabria, Monte Corona, under *Fagus sylvatica* and *Quercus robur*, 16 May 2012, A. Paz & C. Lavoise (IC16051201)*; *ibid.*, 18 Jan. 2013, A. Paz & C. Lavoise (IC18011306)*; Saja, under *Fagus sylvatica*, 29 June 2002, A. Paz & C. Lavoise (IC29060211); *ibid.*, under *Fagus sylvatica*, 12 Sept. 2006, A. Paz & C. Lavoise (IC12090623); *ibid.*, under *Fagus sylvatica* and *Corylus avellana*, 12 Oct. 2008, A. Paz & C. Lavoise (IC12100826); *ibid.*, Cambillas, under *Fagus sylvatica*, 26 July 2008, A. Paz & C. Lavoise (IC26070809); *ibid.*, under *Fagus sylvatica*, 2 Aug. 2008, A. Paz & C. Lavoise (IC02080817); Villar (Campoo), under *Quercus petraea*, 15 Mar. 2004, A. Paz & C. Lavoise (IC15030417); *ibid.*, *Fagus sylvatica* and *Corylus avellana*, 11 July 2011, A. Paz & C. Lavoise (IC11071125); *ibid.*, La Charola, under *Fagus sylvatica* and *Quercus* spp., 27 Apr. 2005, A. Paz & C. Lavoise (IC27040509); *ibid.*, *Pinus* sp., 9 Jan. 2009, A. Paz & C. Lavoise (IC09010915); *ibid.*, under *Castanea sativa*, 5 Mar. 2008, A. Paz & C. Lavoise (IC05030825); *ibid.*, under *Eucalyptus globulus*, 17 Jan. 2012, A. Paz & C. Lavoise (IC17011228); *ibid.*, under *Pinus* sp., 18 Apr. 2011, A. Paz & C. Lavoise (IC18041124); Rioturbo, *Fagus sylvatica*, 28 Apr. 2005, A. Paz & C. Lavoise (IC28040515); *ibid.*, 26 Mar. 2008, A. Paz & C. Lavoise (IC26030817); *ibid.*, mixed forest of *Quercus* sp. and *Fagus sylvatica*, 11 Jan. 2009, A. Paz & C. Lavoise (IC11010916); *ibid.*, *Quercus rubra*, 17 Jan. 2009, A. Paz & C. Lavoise (IC17010903); Hayuela, under *Eucalyptus globulus*, 5 June 2006 (IC05060619); La Molina, under *Quercus robur*, 5 July 2007, A. Paz & C. Lavoise (IC05070721); Saja, Uceda, *Quercus robur*, 23 Nov. 2007, A. Paz & C. Lavoise (IC23110713); *ibid.*, under *Quercus robur*, 20 Apr. 2008, A. Paz & C. Lavoise (IC20030811); Bárcena Mayor, under *Castanea sativa* and *Crataegus monogyna*, 7 May 2008, A. Paz & C. Lavoise (IC07050814); Co, under *Pinus radiata*, 12 Aug. 2008, A. Paz & C. Lavoise (IC12080821); Saja, Bielsa, under *Quercus rubra*, *Corylus avellana* and *Fagus sylvatica*, 18 Apr. 2010, A. Paz & C. Lavoise (IC18041012); San Vicente de la Barquera, under *Eucalyptus* sp., 4 Mar. 2012, A. Paz & C. Lavoise (IC04031227); Huesca, Bielsa, Pineta, Cornato, under *Abies alba*, 2 May 2015 (IC02051502); Málaga, Cortes de la Frontera, La Calderona, *Quercus faginea* and *Quercus suber*, 24 Nov. 2015, A. Paz & C. Lavoise (IC24111504); Navarra, Ultzama, Mycological park Ultzama, *Castanea sativa*, *Fagus sylvatica* and *Corylus avellana*, 22 Oct. 2015, A. Paz & C. Lavoise (IC22101501); Palencia, Guardo, under *Pinus sylvestris*, 7 June 2013, A. Paz & C. Lavoise (IC07061317); Tosandes, under *Quercus ilex*, 5 Oct. 2013, A. Paz & C. Lavoise (IC05101328); Soria, Cuevas de Agreda, under *Quercus faginea* and *Quercus ilex*, 23 Oct. 2015, A. Paz & C. Lavoise (IC23101505). — SWEDEN, Småland, Friesjö, under *Pinus sylvestris*, *Quercus robur*, *Picea abies* and *Fagus sylvatica*, 16 Mar. 2014, L. Hund & A. Molia (AM44-2014, GB-0147063)*.

Notes — A nomenclatural revision of this species, including typifications, will be treated in a separate paper (in prep.).

Elaphomyces granulatus is one of the most common species in the genus, although often confused with *E. asperulus*. Our numerous collections illustrate its wide distribution from Scandinavia to the Mediterranean sea, under broadleaved (*Castanea*, *Corylus*, *Fagus*, *Quercus*) as well as coniferous (especially *Pinus*) trees, and even under introduced trees (*Eucalyptus* spp. and *Pinus radiata*). It is also one of the earliest scientifically named hypogeous fungus, illustrated as '*Tubera cervina*' by L'Obel (1591: pl. 276), who already reported the appetite of cervids for these fungi, known from the Antiquity.

Elaphomyces granulatus has a white peridium, whereas *E. asperulus* displays purplish tinges, a chromatic difference well-supported in our molecular analyses. Some collections observed at UPS in the general herbarium by one of us (A.M.) were obviously composite with a mix of both species. They are often collected together and Fries probably did not separate them. However, purposely or not, Fries (1829) was the first

author restricting the interpretation of *E. granulatus* (formerly known as *E. cervinus*) by describing the peridium as white. The specimens cited by him from the *Stirpes Cryptogamicæ Vogensiaco-Rhenanae* n° 282 (Mougeot & Nestler 1812), studied by us from the centuries kept at LIP, MPU, PC and UPS which represent duplicates of original material (Fries 1829), support the most usual interpretation of *E. granulatus* as retained here, although the UPS collection (revised by A.P. and A.M.) also includes a specimen of *E. hassiacus*. Castellano et al. (2012b) do not interpret *E. granulatus* in the same way but as a synonym of *E. asperulus* (with reddish peridium, contrary to Fries' description), and retain the name *E. leucocarpus* for the species with white inner peridium (and 'spiny-reticulate spores'). All authentic material of *E. leucocarpus* (PC and TO) studied by us represents immature specimens of *E. granulatus* as defined here, with white gleba.

Phylogenetically, *E. granulatus* displays moderate ITS polymorphism (3 nts, Table 2), but the species is well separated from its closest relative *E. asperulus*, as assessed by a D inter min/D intra max ratio = 6 (Table 2).

Two remarkable variants of *E. granulatus* are known to us. One, which will be the object of a separate paper (in prep.), displays a blackish peridial surface and evokes *E. aculeatus* (sect. *Ceratogaster*), although its microscopy is conform to *E. granulatus*. Besides from Scandinavia, this form is known from Corsica (France), with the following collections studied: NORWAY: Oslo, Sognsvann, under *Picea abies*, A. Molia, L. Hund & T. Læssøe, 25 Aug. 2013 (O-21344); Telemark, in mixed forest with *Pinus*, *Corylus avellana* and *Quercus*, 28 Oct. 2013, A. Paz & C. Lavoise (IC28091306); FRANCE: Corse du Sud, Eze, Pont des Cinq Communes, *Castanea sativa*, *Quercus* spp. & *Fagus sylvatica*, 25 Nov. 2014, A. Paz & C. Lavoise (IC25111404); *ibid.*, 26 Nov. 2014, A. Paz & C. Lavoise (IC26111404).

The second variant, recorded from France, Italy and Spain, is phylogenetically indistinguishable from the type, but displays pale spores from the whitish gleba of mature collections. It is introduced below as *E. granulatus* forma *pallidosporus*, forma *nov.*

***Elaphomyces granulatus* forma *pallidosporus* De Vito, F. García, A. Paz & Lavoise, forma *nov.* — MycoBank MB817237; Fig. 4.3, 5f–i**

Etymology. From Latin: *spora* = spore, and *pallidus* = pale, in reference to the pale ascospores.

Holotype. ITALY, Bergama, Dossena, under *Abies pectinata* and *Fagus sylvatica*, 21 July 2011, A. De Vito (LIP 0001132) (Fig. 4.3); isotype in herb. pers. A. Paz (IC21071103)*.

Ascomata irregular, 1.5–5 cm. **Peridial surface** with flat irregular warts. **Peridium** uniform, cream white. **Gleba** light pinkish when mature. **Ascospores** 20–28 µm, almost hyaline.

Additional material studied. FRANCE, Savoie, Mâcot-la-Plagne, forêt domaniale, under *Picea abies* and *Larix decidua*, 25 Aug. 1988, M. Meyer (IC25088801). — SPAIN, Segovia, la Granja, under *Picea abies* and *Pinus* sp., 1 Mar. 1998, F. García (IC01039817).

***Elaphomyces hassiacus* R. Hesse, Hypog. Deutschl. 2: 73. 1894 — Fig. 4.4, 6a–b**

Synonyms. *Elaphomyces cervinus* var. *hassiacus* (R. Hesse) E. Fisch., Rabenh. Krypt.-Fl., ed. 2, 1, 5: 96. 1897.

Elaphomyces asperulus var. *hassiacus* (R. Hesse) Fontana, Mem. Accad. Sci. Torino II, 59: 104. 1909.

Material studied. FRANCE, Savoie, Mâcot-la-Plagne, forêt domaniale, under *Picea abies* and *Larix decidua*, 22 Oct. 1986, M. Meyer (IC22108601); *ibid.*, 18 Sept. 1987, M. Meyer (IC18098701); *ibid.*, 18 Aug. 1988, M. Meyer (IC18088801); *ibid.*, 25 Aug. 1988, M. Meyer (IC25088802); *ibid.*, 4 Nov.



Fig. 6 a–b. *Elaphomyces hassiacus* (IC18111109). a. Ascomata; b. ascospores. — c–i. *Elaphomyces barrioi* (LIP 0001133, holotype). c, e–f. Ascomata; d. ascospores; g–i. details of the peridium. — j–k. *Elaphomyces decipiens*. j. Ascospores (PC, Vittadini); k. ascomata (LIP 0001134, neotype). — Scale bars: a, c, e–f, k = 1 cm; b, d, j = 10 µm; g = 1 mm; h–i = 20 µm. — Photos: a, c, e–f, k. C. Lavoise; b, d, g–j. A. Paz.

1988, *M. Meyer* (IC04118801). — SPAIN, Cáceres, Jarandilla de la Vera, under *Quercus pyrenaica*, 18 Nov. 2011, A. Paz & C. Lavoise (IC18111109)* (Fig. 4.4); Cádiz, El Cuartón, Bosque de Niebla, *Quercus canariensis*, *Quercus pyrenaica* and *Quercus suber*, 23 Nov. 2015, A. Paz & C. Lavoise (IC23111501); *ibid.*, 25 Nov. 2015, A. Paz & C. Lavoise (IC25111505); *ibid.*, 27 Nov. 2015, A. Paz & C. Lavoise (IC27111502); Pelayo, Monte Algameasilla, *Quercus pyrenaica* and *Quercus suber*, 29 Nov. 2015, A. Paz & C. Lavoise (IC29111503); Cantabria, Labarces, under *Quercus robur* and *Fagus sylvatica*, 2 June 2007, A. Paz & C. Lavoise (IC02060712); Logroño, Riva Ruesga, under *Castanea sativa*, 16 May 2012, A. Paz & C. Lavoise (IC16051208).

Notes — The only sequenced collection occupies a unique position in the phylogeny, basal to the whole section in the ITS + 28S combined analysis (Fig. 1) or to the *E. granulatus-asperulus* subclade in the ITS phylogeny (Fig. 2a). Moreover, the remarkably long branch of this collection in the two trees suggests accelerated evolution rate of this species, when compared to other species in the section.

In the description of *E. hassiacus*, Hesse (1894) and Fischer (1897a) mention a bluish inner peridium and a pinkish outer peridium which was considered as a specific feature and that we also observed on our material. However, our observations reveal that *E. asperulus* and *E. hassiacus* both display bluish tinges in the inner peridium at young stages, which turn purplish with age.

Because of their high morphological resemblance, Fontana (1909: 104) concluded that *E. hassiacus* was a variety of *E. asperulus*, a conclusion only provisionally accepted by Dodge (1929: 178). The regularly spiny ascospore ornamentation of *E. hassiacus* appears as the most distinctive feature from *E. asperulus* (Fig. 4). The evanescent cortex makes apparent the macules of the superficial layer of the peridium, as minute opalescent pits spotting the surface of mature specimens.

Elaphomyces* subsect. *Muricati Bellanger & P.-A. Moreau, subsect. nov. — MycoBank MB817238

Holotype. *Elaphomyces muricatus* Fr.: Fr.

Spore ornamentation forming curved rod-like spines. Inner peridium marbled.

Elaphomyces barrioi A. Paz, Lavoise & A. Molia, sp. nov. — MycoBank MB817239; Fig. 4.5, 6c–i

Ascomata 2–5 cm diam. *Peridial surface* with obtuse warts of various heights, light yellow-brown. *Peridium* thick, with marbled aspect, purplish red, forming elliptical spots on vinaceous ground, darker towards gleba. *Asci* subglobose, measuring 30–40 × 40–45 µm, with 2–4 (–6) spores. *Spores* globose, measuring 19–24 µm, ornamented by thick rod-shaped warts, incurved and short, 1.5–2 µm high, confluent at apices forming irregular meshes.

Etymology. Dedicated to the great Spanish mycologist Luis Barrio de la Parte, in honour of his work of sampling, identification and diffusion of his knowledge of hypogaeous fungi. *Gratia, Magister!*

Holotype. SPAIN, Cáceres, Jarandilla de la Vera, under *Quercus pyrenaica*, 16 Dec. 2012, leg. A. Paz & C. Lavoise (LIP 0001133) (Fig. 4.5); isotype in herb. pers. A. Paz (IC16121209)*.

Ascomata globose, yellow when young, turning brown when mature. *Peridial surface* with obtuse, protruding warts inserted with smaller yellow-brown warts. *Peridium* thick, marbled, purplish red, forming ellipsoidal dots on vinaceous ground, darker towards gleba. *Gleba* dark grey-brown with reddish tones. *Smell* intense, rancid-alliaceous. *Warts* of peridial surface made of densely interwoven hyphae, sinuous, thick-walled, yellow-tinged, bound by a coverage of parallel hyphae densely septate, thin-walled, almost colourless, with guttulate content. *Peridium* made of slender hyphae, 2–4 µm wide, sinuous, interwoven, with slight thickenings, slightly light vinaceous-coloured, increasingly pigmented towards gleba to intense vinaceous

colour, darker dots made of strongly coloured red-brown interwoven hyphae. *Gleba* made of branched, septate hyphae, with grey-brown wall. *Asci* globose, containing 2–4 (occasionally 6) ascospores. *Ascospores* globose, measuring 19–24 µm, dark grey-brown, ornamented by thick rod-shaped warts, curved, 1.5–2 µm high, apices confluent and forming irregular meshes.

Additional material studied. FRANCE, Corse du Sud, Pont des Cinq Communes, *Castanea sativa*, *Quercus* sp. and *Fagus sylvatica*, 26 Nov. 2014, A. Paz & C. Lavoise (IC26111423); Meurthe-et-Moselle, Seney-aux-Forges, 23 Dec. 2013, J.-B. Pérez (IC231213-2). — NORWAY, Akershus, Nesodden, Røer, in wooded, rich meadows with *Quercus robur*, 18 Nov. 2011, A. Molia & L. Hund (O-F21187)*; Oslo fylke, Oslo, in broadleaved forest dominated by *Corylus avellana* on rich soil, 12 Mar. 2014, A. Molia & L. Hund (O-F22301)*. — SPAIN, Cádiz, El Cuartón, Bosque de Niebla, *Quercus canariensis*, *Quercus pyrenaica* and *Quercus suber*, 1 Dec. 2015, A. Paz & C. Lavoise (IC01121509); Cantabria, Saja, under *Fagus sylvatica* and *Corylus avellana* on carbonated soil, 5 Sept. 2004, 5 specimens, A. Paz & L. Barrio (IC05090421); Cataluña, Girona, Maganet de Cabreys, under *Castanea sativa*, 17 Nov. 1995, J.M. Vidal (JMV951117-01); Huesca, Torla, Parque Nacional Ordesa y Monte Perdido under *Fagus sylvatica* and *Pinus sylvestris*, 1 May 2015, A. Paz & C. Lavoise (IC01051507); Soria, Cuevas de Agreda, under *Quercus faginea* and *Quercus ilex*, 23 Oct. 2015, A. Paz & C. Lavoise (IC23101503).

Notes — Macroscopically, *E. barrioi* is reminiscent of the *E. muricatus*-complex, from which it differs by the unequal height of the cortical warts. In cross-section, the peridium is marbled, with dark ellipsoidal spots on vinaceous ground, while the *E. muricatus*-group displays a peridium with circular spots on pale ground (cream white). Also distinctive is spore ornamentation, with thick rod-shaped warts, strongly curved and forming loops. It can also be confused with *E. decipiens*, which displays a surface of flat warts slightly staining when touched, and a purplish grey peridium with cream white veins radially oriented up to the outside of the ascome.

Phylogenetically, *E. barrioi* displays moderate ITS polymorphism (2 nts, Table 2), but the species is well separated from its closest relative, provisionally referred to here as '*E. aff. barrioi* 1', as assessed by a D inter min/D intra max ratio > 6 (Table 2).

Elaphomyces decipiens Vittad., Monogr. Tuberacearum: 68. 1831 — Fig. 4.6, 6j–k

Synonyms. *Lycoperdastrum decipiens* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Neotype (here designated MBT374414): SPAIN, Cantabria, Saja, under *Fagus sylvatica*, 28 Jan. 2012, A. Paz & C. Lavoise (LIP 0001134); isoneotype in herb. pers. A. Paz (IC28011203)*.

Elaphomyces variegatus var. *intermedius* Speg., Anales Soc. Ci. Argent. 11: 67. 1881.

Elaphomyces variegatus var. *pallens* Tul. & C. Tul., Fung. Hypog.: 108. 1851.

Elaphomyces verrucosus C.W. Dodge, Ann. Mycol. 27: 171. 1929.

Elaphomyces muricatus forma *fagicola* Ławryn., Flora Polska, Grzyby (Mycota) 18: 134. 1988 (invalid, art. 40.1, no type indicated).

Additional material studied. ITALY, Lombardia, Milano, May 1845, det. C. Vittadini (PC0093893 ex herb. Tulasne, authentic material of *E. decipiens*) (Fig. 4.6); s.loc., s.d., C. Vittadini (PC, herb. C. Montagne CM4383, authentic material of *E. decipiens*). — POLAND, Central Poland, near Łódź, Nature reserve Janinów, in a *Fagus* forest, 7 July 1973, M. Ławrynowicz (LOD 20432, 'type' of *E. muricatus* forma *fagicola*). — PORTUGAL, Figueira de Castelo Rodrigo, *Quercus ilex* and *Juniperus oxycedrus*, 9 Nov. 2015, A. Paz & C. Lavoise (IC09111505). — SPAIN, Asturias, Cuñaba, under *Corylus avellana* and *Castanea sativa*, 12 Sept. 2010, A. Paz & C. Lavoise (IC12091020); San Esteban de Cuñaba, under *Castanea sativa*, 27 Nov. 2011, A. Paz & C. Lavoise (IC27111118)*; Cáceres, Jarandilla de la Vera, under *Quercus petraea*, 18 Nov. 2011, A. Paz & C. Lavoise (IC18111114)*; Cádiz, Los Barrios, Monte Val de Infierno, mixed forest, 21 Nov. 2015, A. Paz & C. Lavoise (IC21111503); El Cuartón, Bosque de Niebla, *Quercus canariensis*, *Quercus pyrenaica* and *Quercus suber*, 25 Nov. 2015, A. Paz & C. Lavoise (IC25111503); *ibid.*, 27 Nov. 2015, A. Paz & C. Lavoise (IC27111503); Cantabria, Monte Corona, under *Fagus sylvatica*, 18 Mar. 2012, A. Paz &

C. Lavoise (IC18031205)*; Caloca, under *Fagus sylvatica*, 31 July 2004, A. Paz & C. Lavoise (IC31070403); Saja, under *Fagus sylvatica*, 30 Mar. 2005, A. Paz & C. Lavoise (IC30030515); *ibid.*, Cambillas, under *Fagus sylvatica*, 1 Apr. 2005, A. Paz & C. Lavoise (IC01040517); *ibid.*, under *Fagus sylvatica*, 26 July 2008, A. Paz & C. Lavoise (IC26070812); Hayuela, under *Eucalyptus globulus*, 5 June 2006, A. Paz & C. Lavoise (IC05060624); Aloños, under *Fagus sylvatica*, 25 June 2008, A. Paz & C. Lavoise (IC25060803); Riva Ruesga, under *Fagus sylvatica*, 12 May 2012, A. Paz & C. Lavoise (IC12051208)*; Málaga, El Palancar, *Quercus suber* and *Quercus canariensis*, 28 Nov. 2015, A. Paz & C. Lavoise (IC28111502). – USA, California, Berkeley, under *Quercus agrifolia*, 20 Nov. 1905, N.L. Gardner (TO, isotype of *E. verrucosus*, Gardner 268).

Notes — The two sequences available in GenBank under this name, generated from Western USA material, clearly represent one or two distinct species (see Fig. 2a and the description of *E. decipiens* by Dodge 1929), that we provisionally refer to here as '*E. aff. barrioi* 1' and '*E. aff. barrioi* 2'. The sequences of *E. decipiens* generated for the present study are clearly distinct from each other and from the sequence DQ974740 of an American collection named '*Elaphomyces muricatus*' (Fig. 2a), building up the phylogenetically most variable species of the whole genus (D intra max = 11 nts, Table 2). Such unusually high ITS polymorphism may reflect closely related cryptic species and splitting the clade accordingly is an option. However, in its current sampling, splitting the *E. decipiens* clade would yield four entities with no or weak statistical support, and each represented by one or two collections only (Fig. 2a). Because neither the morpho-anatomy, nor the ecology or the biogeography of the sampled collections provide any further support for this taxonomic move, we adopt here the inclusive clade, at least provisionally, as *E. decipiens*. Defined this way, the species still displays a D inter min/D intra max ratio = 2 (Table 2) and consequently, it is compatible with ITS DNA barcoding. *Elaphomyces decipiens* has a wide distribution in the Northern Hemisphere, further supported by the morphological study of an isotype of *E. verrucosus* C.W. Dodge (TO) from California, found to be identical to European collections of *E. decipiens*.

The high ITS polymorphism of *E. decipiens* contrasts with the low morphological variability of all collections and makes it an easily recognizable species in the field. However, several collections repeatedly made under *Fagus sylvatica* were distinct by a nearly smooth peridial surface, and correspond to a form attributed to *E. muricatus* by Fontana (1909) and as '*E. muricatus* forma *facicola*' by Ławrynowicz (1988). No significant difference could be found in our DNA analyses among all these collections.

***Elaphomyces muricatus* Fr.: Fr. var. *muricatus* in Fries, Syst. Mycol. 3: 59. 1829 — Fig. 4.7, 7a–b**

Synonyms. *Ceraunium muricatum* (Fr.: Fr.) Wallr., Fl. Crypt. Germ.: n° 2288. 1833.

Elaphomyces vulgaris α *muricatus* (Fr.: Fr.) Corda, Deutschl. Fl. III, 19–20: 21. 1841.

Lycoperdon scabrum Willd., Fl. Ber. Prodr.: 409. 1787.

Scleroderma cervinum β [unranked] *scabrum* (Willd.) Pers., Syn. Meth. Fung.: 157. 1801.

Elaphomyces cervinus β [unranked] *scaber* (Willd.) Schltdl., Fl. Berol. 2: 167. 1824.

Ceraunium scabrum (Willd.) Wallr., Fl. Crypt. Germ. 2: 406. 1833.

Elaphomyces granulatus var. *scaber* (Willd.) Rabenh., Deutschl. Krypt.-Fl. 1: 290. 1844.

Elaphomyces scaber (Willd.) J. Schröt., Krypt.-Fl. Schlesien 3: 223. 1893.

Elaphomyces hirtus Tul. & C. Tul., Ann. Sci. Nat. Bot. sér. II, 16: 23. 1841.

Elaphomyces variegatus var. *hirtus* (Tul. & C. Tul.) Tul. & C. Tul., Fung. Hypog.: 108. 1851.

Elaphomyces muricatus var. *hirtus* (Tul. & C. Tul.) Qué., Mém. Soc. Émul. Montbéliard, sér. 2, 5: 380. 1873.

Elaphomyces variegatus var. *anceps* Speg., Anales Soc. Ci. Argent. 11: 67. 1881.

Material studied. FRANCE, 'dans les forêts autour de Paris', 1841, L.-R. Tulasne & C. Tulasne (PC, herb. C. Montagne CM4388, original material of *E. hirtus*); Hauts-de-Seine, Meudon ('in sylvis Meudon'), 1841, L.-R. Tulasne & C. Tulasne (PC 0096805, herbier général ex herb. Tulasne, original material of *E. hirtus*); s.loc., s.d. (TO, coll. O. Mattioli, 'autopici' ex PC) (Fig. 4.7). – ITALY, s.loc., 1909, Soffietti (TO, coll. O. Mattioli, as '*E. hirtus*'). – NORWAY, Nordland, Saltdalen, Bleiknesmo, flat, sandy *Pinus* forest with some *Betula*, 11 Aug. 2012, R. Kristiansen (O-F245291)*; Vesterøy: Guttormsvaun, in *Quercus* forest, 23 Sept. 2011, A. Molia & L. Hund (O-F245437); Akershus: Nesodden, Røer, semirich *Quercus* forest, 18 Nov. 2011, A. Molia & L. Hund (O-F21009); *ibid.*, in mixed rich forest with *Quercus* dominance (+ *Picea* and *Pinus*), 18 Nov. 2011, A. Molia & L. Hund (O-F22087). – PORTUGAL, Figueira de Castelo Rodrigo, *Quercus ilex* and *Juniperus oxycedrus*, 9 Nov. 2015, A. Paz & C. Lavoise (IC09111504); Mata do Bussaco, mixed forest, 11 Nov. 2015, A. Paz & C. Lavoise (IC11111504). – SPAIN, Asturias, Cuñaba, under *Castanea sativa* and *Corylus avellana*, 7 Jan. 2010, A. Paz & C. Lavoise (IC07011024); *ibid.*, under *Betula pendula*, 10 Apr. 2011, A. Paz & C. Lavoise (IC10041123); Covadonga, under *Corylus avellana*, 13 Mar. 2010, A. Paz & C. Lavoise (IC13031012); San Esteban de Cuñaba, under *Castanea sativa* and *Fagus sylvatica*, 6 Mar. 2011, A. Paz & C. Lavoise (IC06031126); *ibid.*, under *Castanea sativa* and *Quercus* sp., 14 Apr. 2013, A. Paz & C. Lavoise (IC14041301)*; Somiedo, under *Corylus avellana* and *Quercus* sp., 15 May 2012, A. Paz & C. Lavoise (IC15051231); Cádiz, Los Barrios, Monte Val de Infierno, mixed forest, 21 Nov. 2015, A. Paz & C. Lavoise (IC12111502); Cantabria, Monte Corona, under *Eucalyptus globulus*, 1 Apr. 2013, A. Paz & C. Lavoise (IC01041301)*; *ibid.*, under *Fagus sylvatica* and *Quercus robur*, 13 Mar. 2004, A. Paz & C. Lavoise (IC13030417); Bielsa, under *Pinus radiata*, 3 Mar. 2012, A. Paz & C. Lavoise (IC03031214)*; Bárcena Mayor, under *Quercus petraea*, 26 Aug. 2004, A. Paz & C. Lavoise (IC26080406); *ibid.*, under *Castanea sativa* and *Crataegus monogyna*, 7 May 2008, A. Paz & C. Lavoise (IC07050814); Monte Corona, under *Quercus rubra*, 12 Feb. 2005, A. Paz & C. Lavoise (IC12020510); *ibid.*, under *Castanea sativa*, 26 Feb. 2005, A. Paz & C. Lavoise (IC26020513); Hayuela, under *Abies alba*, 14 June 2005, A. Paz & C. Lavoise (IC14060515); Uceda, under *Quercus robur*, 23 Nov. 2007, A. Paz & C. Lavoise (IC23110704); Bielsa, La Charola, under *Castanea sativa*, 9 Jan. 2009, A. Paz & C. Lavoise (IC09010913); *ibid.*, under *Pinus* sp., 2 Mar. 2008, A. Paz & C. Lavoise (IC02030827); Rioturbio, under *Fagus sylvatica*, 26 Mar. 2008, A. Paz & C. Lavoise (IC26030817); Aloños, under *Pinus radiata*, 25 June 2008, A. Paz & C. Lavoise (IC25060828); Huesca, Torla, Parque Nacional Ordesa y Monte Perdido, under *Fagus sylvatica* and *Pinus sylvestris*, 1 May 2015, A. Paz & C. Lavoise (IC01051506); Navarra, Ultzama, Mycological park Ultzama, *Castanea sativa*, *Fagus sylvatica* and *Corylus avellana*, 22 Oct. 2015, A. Paz & C. Lavoise (IC22101502); Palencia, Tosandes, under *Quercus ilex*, 1 Oct. 2012, A. Paz & C. Lavoise (IC01101205); Segovia, Pedrosa, under *Fagus sylvatica*, 28 Apr. 2013, A. Paz & C. Lavoise (IC28041325); Soria, Cuevas de Agreda, under *Quercus faginea* and *Quercus ilex*, 23 Oct. 2015, A. Paz & C. Lavoise (IC23101504).

Notes — Nomenclatural analysis of this species, including typifications, will be treated in a separate paper (in prep.).

Elaphomyces muricatus is widespread and common in Europe, with a wide morphological variability that prompted the authors of the 19th century to recognize different species such as *E. reticulatus*, *E. hirtus* or *E. variegatus*. These variants can be recognized according to the aspect of the peridium or the presence of a basal depression (Ceruti 1960, Ławrynowicz 1988), congruent with divergences in ITS sequences (Fig. 2) although these divergences are low, and two of them (*reticulatus* and *variegatus*) are recognized here at varietal rank.

The original material of *E. hirtus* found in C. Montagne's herbarium (PC) is represented by two well-preserved specimens. The largest specimen is recognised as a typical *E. muricatus*, but the smallest one, not fully mature, slightly darker, has the smallest spores observed in the section and might represent a rare small-spored form of *E. muricatus*, not yet recorded. The two other original collections kept at PC (herbarium Tulasne, merged in the Herbier Général) have large spores as described by Tulasne & Tulasne (1841, 1851), and therefore can be fully assimilated to *E. muricatus*.

Phylogenetically, *E. muricatus* displays relatively high ITS polymorphism (5 nts, Table 2) but the lowest D inter min value of the whole study (9 nts, Table 2), making it incompatible with genus-



Fig. 7 a–b. *Elaphomyces muricatus* var. *muricatus*. a. Ascomata (O-F245291); b. ascospores (PC, Vittadini). — c–d. *Elaphomyces muricatus* var. *reticulatus* (LIP 0001153, epitype). c. Ascospores; d. ascomata. — e–f. *Elaphomyces muricatus* var. *variegatus*. e. Ascomata (LIP 0001154, epitype); f. ascospores (PC, Vittadini). — Scale bars: a, d–e = 1 cm; b–c, f = 10 μ m. — Photos: a, d–e. C. Lavoise; b–c, f. A. Paz.

wide ITS barcoding (see below and Fig. 3). Its sister species, referred to here as *E. aff. muricatus*, is nonetheless considered as a separate unit based on strict phylogenetic bases, it fulfils species recognition criteria (Materials and Methods). Future studies and deeper sampling of the latter clade are necessary to identify the putative morpho-anatomic diagnostic features of this so far cryptic sister species.

Elaphomyces muricatus* var. *reticulatus (Vittad.) A. Paz & Lavoise, *comb. & stat. nov.* — MycoBank MB817240; Fig. 4.8, 7c–d

Basionym. *Elaphomyces reticulatus* Vittad., Monogr. Lycoperd.: 74. 1842.

Synonym. *Elaphomyces muricatus* forma *reticulatus* (Vittad.) Ławryn., Flora Polska, Grzyby (Mycota) 18: 134. 1988.

Lectotype (here designated MBT374415): iconotype Vittadini, Monogr. Lycoperd.: pl. III, f. X. 1842.

Epitype (here designated MBT374416): SPAIN, Cantabria, Saja, under *Fagus sylvatica* and *Corylus avellana*, 14 Jan. 2012, A. Paz & C. Lavoise (LIP 0001153) (Fig. 4.8); isoeotype in herb. pers. A. Paz (IC14011206)*.

Material studied. NORWAY, Frogn, Knardal, in rich, mixed forest with *Corylus avellana*, *Tilia cordata* etc., 2013, A. Molia, L. Hund & K. Killingmo (AM134-2013, O-F21357). — SPAIN, Labarces, under *Castanea sativa*, *Fagus sylvatica* and *Quercus* sp., 2 June 2007, A. Paz & C. Lavoise (IC02060728); Saja, *Corylus avellana*, 6 July 2008, A. Paz & C. Lavoise (IC06060833); *ibid.*, under *Castanea sativa*, 13 Nov. 2011, A. Paz & C. Lavoise (IC13111123); *ibid.*, under *Corylus avellana* and *Fagus sylvatica*, 22 Dec. 2013, A. Paz & C. Lavoise (IC22121307); Monte Corona, under *Fagus sylvatica*, 24 May 2012, A. Paz & C. Lavoise (IC24051229); *ibid.*, under *Fagus sylvatica*, 3 May 2012, A. Paz & C. Lavoise (IC03051209)*; Córdoba, Priego de Córdoba, Pinar del puente San Juan, *Pinus pinea* and *Pinus pinaster*, 25 May 2015, A. Paz & C. Lavoise (IC25051502).

Notes — This variety represents an apparently stable and well-defined aspect of *E. muricatus*, with low, hardly distinct warts, and peridium slightly marbled in cross-section, light at first and darkening when drying.

Elaphomyces muricatus* var. *variegatus (Vittad.) A. Paz & Lavoise, *comb. & stat. nov.* — MB817241; Fig. 4.9, 7e–f

Basionym. *Elaphomyces variegatus* Vittad., Monogr. Tuberacearum: 68. 1831.

Synonyms. *Elaphomyces muricatus* forma *variegatus* (Vittad.) Ceruti, Iconogr. Mycol. (Milan) 28: 6. 1960.

Lectotype (here designated MBT374452): iconotype Vittadini, Monogr. Tuberacearum: pl. IV, f. IV. 1831.

Epitype (here designated MBT374453): SPAIN, Cantabria, Saja, under *Fagus sylvatica*, 5 Jan. 2013, A. Paz & C. Lavoise (LIP 0001154); isoeotype in herb. pers. A. Paz (IC05011307)*.

Elaphomyces variegatus var. 'd' *coelatus* Tul. & C. Tul., Fung. Hypog.: 108. 1851.

Elaphomyces coelatus (Tul. & C. Tul.) Bigeard & H. Guill., Fl. Champ. Sup. France: 566. 1909.

Material studied. FRANCE, Hauts-de-Seine, Clamart, 'vere 1841' (PC, herbier général, ex herb. Tulasne, as '*E. variegatus caelatum* Tul.'): lectotype of *E. variegatus* var. *coelatus*, see above) (Fig. 4.9). — ITALY (?), s.loc., s.d., C. Vittadini (TO, as '*E. variegatus*', authentic material); *ibid.*, TO, as '*E. decipiens* Vitt.?' — NORWAY, Østfold, Borge, N-Ø for Begby, in *Quercus* forest, 9 Sept. 2012, A. Molia, L. Hund & R. Kristiansen (AM42-2014, O-F245312)*; Oppegård, Svartskog (by the church), rich deciduous forest with *Quercus*, *Corylus* etc., 13 Nov. 2011, L. Hund & A. Molia (AM152, O-F21007)*. — SPAIN, Asturias, San Esteban de Cuiñaba, under *Castanea sativa*, 10 Apr. 2011, A. Paz & C. Lavoise (IC10041137); Somiedo, under *Fagus sylvatica* and *Corylus avellana*, 4 June 2013, A. Paz & C. Lavoise (IC04061321); Cantabria, Saja, under *Fagus sylvatica* and *Corylus avellana*, 23 July 2011, A. Paz & C. Lavoise (IC23071117)*; Navarra, Ultzama, Mycological park Ultzama, *Castanea sativa*, *Fagus sylvatica* and *Corylus avellana*, 22 Oct. 2015, A. Paz & C. Lavoise (IC22101503). — SWEDEN, Småland, Femsjö, under *Picea abies*, *Pinus sylvestris* and *Betula pendula*, 15 Mar. 2014, L. Hund & A. Molia (AM43-2014, GB-0147062)*.

Notes — This variety is characterized by ascocarps with a distinct basal depression, peridial surface marbled by broad discoloured plages, and peridium 2–5 mm thick, lighter-coloured in cross-section.

Elaphomyces quercicola Ławryn., A. Paz & Lavoise, *sp. nov.* — MycoBank MB817242; Fig. 4.10, 8a–e

Based on *E. muricatus* forma *quercicola* Ławryn. 1988. Flora Polska, Grzyby (Mycota) 18: 134 (invalid, McNeill et al. 2012, art. 40.1: no type indicated).

Differs from *E. muricatus* by larger ascomata up to 50 mm diam, with strongly adherent debris and mycelial cords, and by peridial surface with large, acute and equal warts. Spores 19–25 µm wide, rod-like warts isolated, thick and curved.

Etymology. From Latin, *Quercus* = oak, and *cola* = inhabitant, associated with, in reference to its frequent occurrence under *Quercus* spp.

Holotype. SPAIN, Cantabria, Saja, under *Quercus petraea*, 23 July 2011, A. Paz & C. Lavoise (LIP 0001155); isotype in herb. pers. A. Paz (IC23071107)* (Fig. 4.10).

Ascomata 20–50 mm diam. *Outer peridium* with pyramid-like warts regularly alternated with conical or obtuse warts, shiny orange-brown, embedded into a mycelial coating formed by hyphae, mycorrhizae and plant remnants, adherent and hardly separable from the peridium. *Inner peridium* thick, marbled by irregular reddish brown dots, gradually darker towards gleba, surrounded by thin white veins. *Gleba* grey-brown with intense reddish tone. Smell intense, fungoid and of garlic.

Outer peridium (warts) formed by densely interwoven hyphae, thick-walled, reddish and sinuose. *Inner peridium* made of an irregular assemblage of densely interwoven hyphae; veins formed by irregularly sinuate, thin-walled, colourless hyphae; dots formed by groups of reddish coloured hyphae with irregularly thickened wall. *Gleba* formed by branched and septate hyphae, with grey-brown wall. *Asci* subglobose, containing 2–4 ascospores (occasionally 6–8). *Ascospores* globose, 19–25 µm, with short isolated rod-shaped spines, very thick and strongly curved, bow-shaped at last. Usually under *Quercus* spp., widespread in continental Europe.

Additional material studied. POLAND, Central Poland, near Nowe Miasto, Nature reserve Trębaczew, under *Quercus robur*, 21 May 1969, M. Ławryniewicz (LOD 20335, 'type' of *E. muricatus* forma *quercicola*) (Fig. 4.10). — SPAIN, Cantabria, Barcena Mayor, under *Quercus pubescens*, 23 July 2011, A. Paz & C. Lavoise (IC23071104)*; Monte Corona, *Quercus rubra*, 3 Mar. 2012, A. Paz & C. Lavoise (IC03031216); Arenas de Iguña, under *Quercus petraea*, 8 May 2013, A. Paz & C. Lavoise (IC08051322); Huesca, Bielsa, Pineta, Cornato, under *Abies alba*, 2 May 2015, A. Paz & C. Lavoise (IC02051501).

Notes — This species is for the first time recognized as distinct from *E. muricatus*, with the support of rDNA phylogenies (Fig. 1, 2a). These analyses reveal that some features are more taxonomically informative than previously thought: spores with small curved, hook-like spines, large cleistothecia with bright orange cortex of pyramidal warts, a regular alternate of high and flat warts, and a mycelial crust extremely adherent and difficult to separate from the cortex. To our knowledge, since its description by Ławryniewicz (1988) only one new collection from France has been reported, by Pérez & Lilbert (2014).

Phylogenetically, the autonomy of *E. quercicola* from *E. muricatus* is supported by a virtually infinite D inter min/D intra max ratio (D intra max = 0 nt, Table 2). However, it should be pointed out that the D inter min value of the species lies just below the barcode gap of the genus (see Table 2 and Fig. 3), preventing the two species to be resolved by a genus-wide ITS barcoding approach.



Fig. 8 a–e. *Elaphomyces quercicola* (LIP 0001155, holotype). a. Ascospores (LOD 20335); b, d–e. ascomata; c. details of the peridium. — f–l. *Elaphomyces violaceoniger* (LIP 0001135, holotype). f, h–i. Ascomata; g. ascospores, j–l. details of the peridium. — Scale bars: a, g = 10 µm; b, d–f, h–i = 1 cm; c, j–l = 20 µm. — Photos: b, d–f, h–i. C. Lavoise; a, c, g, j–l. A. Paz.

***Elaphomyces violaceoniger* A. Paz, F. García & Lavoise, sp. nov.** — MycoBank MB817245; Fig. 4.11, 8f–l

Differs from *E. barrioi* by peridial surface of truncate warts, confluent by 2–6 at base and forming well-delimited patches, peridium darker, marbled with large dark purple to blackish ellipsoid spots on pale vinaceous ground, darker towards gleba, and spores ornamented by thick rod-like warts with apices confluent and drawing braids when mature.

Etymology. From Latin, *violaceus* = purple, and *niger* = black, in reference to the characteristic colours of inner peridium and peridial surface, respectively.

Holotype. SPAIN, Segovia, Cuellar, under *Quercus ilex*, 22 Feb. 2014, F. García (LIP 0001135) (Fig. 4.11); isotype in herb. pers. A. Paz (IC22021401)*.

Ascomata globose, yellow when young, turning yellow-brown when mature. **Peridial surface** with irregular, truncate warts, clustered by 2–6 at base and forming well-delimited patches. **Peridium** thick, marbled, with ellipsoidal dark purple to blackish spots on light purplish ground, gradually darker towards gleba. **Gleba** dark purplish brown. **Smell** weak, of garlic. Warts of peridial surface made of densely interwoven hyphae, thick-walled, bright yellow-tinged, linked at base by tangential colourless hyphae, thick-walled, abundantly septate. **Peridium** made of slender hyphae, 3–5 µm wide, sinuous, interwoven, locally slightly widened, pinkish purple-tinged, with locally darker to nearly black-coloured hyphae, broader towards gleba. **Spores** globose, 22–24 µm diam, ornamented by thick rod-like warts 1.5–2 µm high, curved, apices confluent and drawing braids when mature.

Additional material studied. NORWAY, Oslo, Østensjøvannet, deciduous forest with *Corylus avellana* etc. on rich soil, 15 Mar. 2014, A. Molia & L. Hund (IC15031401)*. — SPAIN, Burgos, Villandiego, under *Quercus ilex*, 9 May 2014, A. Paz & C. Lavoise (IC9051425); *ibid.*, 21 Oct. 2015, A. Paz & C. Lavoise (IC21101507); Segovia, Orejana, under *Quercus ilex*, 24 Oct. 2015, A. Paz & C. Lavoise (IC24101501); Soria, Cueva de Agreda, *Quercus ilex* and *Quercus sp.*, 23 Oct. 2015, A. Paz & C. Lavoise (IC23101506).

Notes — Macroscopically, *E. violaceoniger* strongly evokes *E. muricatus*, but differs by peridial warts truncate, welded by 2–6 and forming isolated patches. The dark purplish peridium distinguishes this species from all other in the *E. muricatus*-group which display a peridium marbled by circular dots on pale (cream-white) ground. The spores with typical ornamentation forming braids at maturity is also distinctive. Differences with *E. decipiens* are the flat warts of the latter, which slightly stain when touched, and peridium grey vinaceous purple marbled with white veins. The most similar species, *E. barrioi*, differs by obtuse peridial warts, well-delimited from each other, of unequal height, by peridium with small purplish red ellipsoidal dots on lighter vinaceous ground, and by the ornamentation of spores forming irregular meshes instead of braids.

***Elaphomyces* subsect. *Papillati* Bellanger & P.-A. Moreau, subsect. nov.** — MycoBank MB817246

Spore ornamentation of crested type.

Type. *Elaphomyces papillatus* Vittad.

***Elaphomyces papillatus* Vittad. var. *papillatus* in Vittadini, Monogr. Tuberacearum: 64. 1831 — Fig. 4.12, 9a–b**

Synonyms. *Lycoperdastrum papillatum* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374417): iconotype, Vittadini, Monogr. Tuberacearum: pl. IV, f. 3. 1831 (only certified original material).

Epitype (here designated MBT374418): SPAIN, Cantabria, Riva Ruesga, under *Fagus sylvatica* and *Corylus avellana*, 12 May 2012, A. Paz & C. Lavoise (LIP 0001136); isoeotype in herb. pers. A. Paz (IC12051202)*.

***Elaphomyces variegatus* var. *fuscescens* Speg. ex Sacc., Michelia 1, 4: 416. 1878.**

Additional material studied. ITALY (?), s.loc., s.d., C. Vittadini (PC0093931 ex herb. Tulasne, authentic material of *E. papillatus*); *ibid.* (TO, authentic material of *E. papillatus*, ex PC) (Fig. 4.12). — SPAIN, Asturias, San Esteban de Cuñaba, under *Fagus sylvatica* and *Castanea sativa*, 26 May 2012, A. Paz & C. Lavoise (IC26051201)*; Cantabria, Caloca, under *Fagus sylvatica* and *Corylus avellana*, 11 June 2011, A. Paz & C. Lavoise (IC11061136); Arenas de Iguña, under *Corylus avellana* and *Betula pendula*, 8 May 2013, A. Paz & C. Lavoise (IC08051327); Monte Corona, *Fagus sylvatica* and *Castanea sativa*, 9 July 2013, A. Paz & C. Lavoise (IC09071308); Saja, under *Fagus sylvatica* and *Corylus avellana*, 26 July 2008, A. Paz & C. Lavoise (IC26070803)*; *ibid.*, under *Corylus avellana*, 22 Dec. 2013, A. Paz & C. Lavoise (IC22121327); *ibid.*, under *Corylus avellana*, 6 July 2011, A. Paz & C. Lavoise (IC06071105)*; Parque Natural del Asón, under *Corylus avellana*, 15 Sept. 2012, A. Paz & C. Lavoise (IC15091207); Segovia, La Pinilla, under *Fagus sylvatica*, 24 Oct. 2011, F. García (IC24091105).

Notes — This species is easily recognized by its unique combination of characters, especially the small, pale spores ornamented with linear crests. However, important variability of other macro- and microscopic features led to the distinction of two ‘species’, namely *E. sulphureopallidus* in Central Europe and *E. striatosporus* in Scandinavia. The phylogenetic analysis of all these collections supports three varieties with morpho-anatomical and biogeographical distinct features (see Fig. 2a and below).

***Elaphomyces papillatus* var. *striatosporus* (Kers) A. Paz & Lavoise, comb. & stat. nov.** — MycoBank MB817247; Fig. 4.13, 9c–e

Basionym. *Elaphomyces striatosporus* Kers, Bot. Not. 133, 2: 149. 1980.

Material studied. NORWAY, Møre og Romasdal, Nesset, Eikesdal, under Rangåfjellet, in deciduous forest with *Corylus avellana* on semi-rich soil, 17 Sept. 2011, K. Killingmo, K. Hund, V. Hund, A. Molia & M. Jeppson (AM35, O-F21185)* (Fig. 4.13); Nord-Trøndelag, Inderøy, Råvika, in deciduous forest under *Corylus avellana* on rich soil, 21 Oct. 2011, A. Molia & L. Hund (AM76, O-F21184)*; Oslo, Bygdøy, Klausåsen, in deciduous forest under *Corylus avellana* on rich soil, 21 Sept. 2012, K. Killingmo, K. Hund & A. Molia (O-F245333)*; *ibid.*, S of Rodeløkken Kafe, in calcareous pasture under *Tilia cordata*, 21 Sept. 2012, K. Killingmo, K. Hund & A. Molia (O-F245330)*; *ibid.*, Hovedøya, calcareous deciduous forest (*Corylus*, *Tilia*, *Quercus*, *Betula* and *Pinus*), 23 Sept. 2012, K. Killingmo, K. Hund, V. Hund, L. Hund, M. Mowinckel-Amundsen & A. Molia (O-245337)*.

Notes — These Norwegian collections are referred to as a variety of *E. papillatus* through DNA analyses (Fig. 2a), differing from the type by spore ornamentation and peridial surface. Other differences pointed out by Kers (1980), such as size and colour of the peridium, are not constant in some localities where the species is abundant.

***Elaphomyces papillatus* var. *sulphureopallidus* P.-A.**

Moreau, A. Paz, Lavoise & J.M. Vidal, var. nov. — MycoBank MB817248; Fig. 4.14, 9f–g

Asocarps 5–30 mm diam, of bright yellow colour. Peridial surface practically smooth with small reddish areoles. **Peridium** 1.5–2 mm thick, grey with faint bluish tone. **Gleba** pinkish cream. **Spores** 13–16 µm, with branched and daedaloid crests like in var. *papillatus* but hyaline.

Etymology. From Latin, *sulphureus* = sulphur-like, and *pallidus* = pale, in reference of the uniformly pale yellow colour of asocarps.

Holotype. SPAIN, Asturias, San Esteban de Cuñaba, under *Castanea sativa* and *Fagus sylvatica*, 13 May 2012, A. Paz & C. Lavoise (LIP 0001156); isotype in herb. pers. A. Paz (IC13051212)* (Fig. 4.14).

Notes — Our only collection differs morphologically from typical collections of *E. papillatus* and could be interpreted as a pale, smoothened deviant collection, but it is also deviant in its ITS sequences by two substitutions and one insert, which is also the case of var. *striatosporus* (Fig. 2a). At first, this collection was morphologically identified to Vacek's (1949: 57)



Fig. 9 a–b. *Elaphomyces papillatus* var. *papillatus*. a. Ascospores (TO, Vittadini); b. ascomata (LIP 0001136, epitype). — c–e. *Elaphomyces papillatus* var. *striatosporus*. c–d. Ascomata (AM35–2014); e. ascospores (O). — f–g. *Elaphomyces papillatus* var. *sulphureopallidus* (LIP 0001132, holotype). f. Ascomata; g. ascospores. — Scale bars: a, e, g = 10 µm; b, d, f = 1 cm; c = 0.5 cm. — Photos: a, d–e, g. A. Paz; b, c, f. C. Lavoise.



Fig. 10 a–b. *Elaphomyces cyanosporus*. a. Ascospores (PC, lectotype); b. ascomata (LIP 0001137, epitype). — c–d. *Elaphomyces foetidus*. c. Ascomata (LIP 0001138, epitype); d. ascospores (K(M) 162153, lectotype). — e–f. *Elaphomyces persoonii*. e. Ascospores (PC, Vittadini); f. ascomata (LIP 0001139, epitype). — Scale bars: a, d–e = 10 μ m; b–c, f = 1 cm. — Photos: a, d–e. A. Paz; b, c, f. C. Lavoise.

description of '*Elaphomyces sulphureopallidus*', but the revision of the type of this species revealed that it is not an *Elaphomyces* (see Excluded species below). By reference to this author and as a tribute to his remarkable work on hypogeous fungi, we chose to attribute to this new variety the same epithet he first introduced.

Elaphomyces* sect. *Ascoscleroderma (Clémencet) Bellanger & P.-A. Moreau, *stat. nov.* — MycoBank MB817249

Basionym. *Ascoscleroderma* Clémencet, *Botaniste* 24: 12. 1932 (genus).

Holotype. *Elaphomyces cyanosporus* Tul. & C. Tul. (Clémencet 1932).

Notes — In the original publication (Corda 1841: 51), the genus *Phlyctospora* was based on *P. fusca*, univocally interpreted after Beck (1889) as a *Scleroderma* (*Basidiomycota*, *Boletales*) and supported by an explicit plate (Corda 1841: pl. 16; 1842: pl. 37, f. 4), but he also included *E. persoonii*, not cited in the protologue but several pages earlier (Corda 1841: 22). Dodge (1929: 158) and all subsequent authors retain the first element (*P. fusca*) as the type species of the genus, what is also accepted here; nonetheless, Dodge (1929: 159) defines a subsection *Phlyctospora*, attributed to Zobel, by a sterile base and including *E. cyanosporus*, *E. foetidus* and *E. persoonii*.

Clémencet's (1932) detailed study of *E. cyanosporus* also points out the differentiated base with mycelial tuft, a character less (if even) developed in the two other species with reticulate spores cited below. This differentiated base could be interpreted as homologous to the pseudostipe of *Pseudotulostoma volvatum* and to its sessile relative *E. adamizans* (Castellano et al. 2016), but the ITS + 28S analyses (Fig. 1) do not support such a relationship and places the two neotropical species in basal position within the *Ascoscleroderma*/Malacodermei clade, consistent with Castellano et al. (2016).

Elaphomyces cyanosporus Tul. & C. Tul., *Fung. Hypog.*: 113. 1851 — Fig. 4.15, 10a–b

Basionym. *Elaphomyces persoonii* forma *minor* Tul. & C. Tul., *Ann. Sci. Nat., Bot. Sér. II*, 16: 25. 1841.

Synonyms. *Phlyctospora cyanospora* (Tul. & C. Tul.) Zobel in Corda, *Icon. Fungorum* 6: 52. 1854.

Lycoperdastrum cyanosporum (Tul. & C. Tul.) Kuntze, *Revis. Gen. Pl.* 2: 858. 1891.

Lectotype (here designated MBT374419): FRANCE, Hauts-de-Seine, Meudon, summer 1841, coll. Tulasne (PC, herbier général) ('*Elaphomyces persoonii* Vittad. var. *minor* Tul. in castanetis, Meudon prope Paris, estate, 1841, T.'; later addition by Tulasne: '*Elaphomyces cyanosporus* Tul. F. Hypog. c. icone') (Fig. 4.15).

Epitype (here designated MBT374420): SPAIN, Asturias, San Esteban de Cufiaba, under *Castanea sativa*, 27 Nov. 2012, A. Paz & C. Lavoise (LIP 0001137); isoeotype in herb. pers. A. Paz (IC27111203)*.

Additional material studied. FRANCE, Hauts-de-Seine, Meudon, in castanetis, estate 1841 (PC ex herb. Tulasne, as '*E. persoonii* β *minor*', authentic material); s.loc. (TO, coll. O. Mattiolo, ex herb. PC, 'autoptici'). — ITALY, Torino, 1909, Soffietti (TO, A. Druent). — PORTUGAL, Figueira de Castelo Rodrigo, *Quercus ilex* and *Juniperus oxycedrus*, 9 Nov. 2015, A. Paz & C. Lavoise (IC09111502); Mata do Bussaco, mixed forest, 11 Nov. 2015, A. Paz & C. Lavoise (IC11111505). — SPAIN, Cádiz, Los Barrios, Monte Val de Infierno, mixed forest, 21 Nov. 2015, A. Paz & C. Lavoise (IC211115014); Cantabria, Uceda, under *Quercus pubescens*, 18 Apr. 2012, A. Paz & C. Lavoise (IC18041207)*; Bárcena Mayor, under *Castanea sativa* and *Crataegus monogyna*, 7 May 2008, A. Paz & C. Lavoise (IC07050817); Arenas de Iguña, under *Quercus petraea*, 21 May 2008, A. Paz & C. Lavoise (IC21050830); Monte Corona, under *Fagus sylvatica* and *Quercus rubra*, 29 Oct. 2011, A. Paz & C. Lavoise (IC29101108).

Notes — Three parts in the Tulasne herbarium (PC, *herbier général*, filed as '*E. persoonii*') are labelled 'Meudon, estate 1841' and likely belong to the same original gathering, of which

one is designated here as lectotype. Another part of this collection is kept in M.J. Berkeley's collections (K 162168, as '*Elaphomyces persoonii* var. *minor*'). Five other envelopes labelled '*E. cyanosporus*' by Tulasne (PC, not revised) are posterior to 1841; a last authentic collection, rich and well-preserved but not dated, is kept as '*E. cyanosporus*' ('*Elaphomyces cyanosporus* Tul., Meudon', handwritten by Tulasne, PC, from herb. Roussel).

Because *E. cyanosporus* is explicitly published as a *nomen novum* by Tulasne & Tulasne (1851: 113) for the previously published *E. persoonii* forma *minor*, these names are nomenclatural synonyms (Trappe 1969: 171).

Phylogenetically, the two sequenced collections of *E. cyanosporus* display low ITS polymorphism and long D inter min (1 nt and 24 nts, respectively, Table 2), strongly supporting the autonomy of the species. Moreover, in light of what precedes, it is worth noting that *E. persoonii* is only distantly related to this species and does not display sister-clade relationships with it, in either of our analyses (Fig. 1, 2c). Thus, the initial rank proposed for *E. cyanosporus* as a form of *E. persoonii* is not supported phylogenetically and the distinct evolutionary history of these two taxa fully deserves their own specific rank.

Elaphomyces foetidus Vittad., *Monogr. Lycoperd.*: 81. 1842 — Fig. 4.16, 10c–d

Synonym. *Lycoperdastrum foetidum* (Vittad.) Kuntze, *Revis. Gen. Pl.* 2: 858. 1891.

Lectotype (here designated MBT374421): ITALY (?), s.loc., s.d., C. Vittadini (K(M) 162153, coll. M.J. Berkeley, half an ascome, as '*Elaphomyces graveolens* Vitt.'). Isolectotypes (parts of the same ascocarp): s.loc., s.d., C. Vittadini (PC, ex herb. Tulasne); ibid. (TO, 'autoptico', ex PC).

Epitype (here designated MBT374422): SPAIN, Cáceres, Jarandilla de la Vera, under *Quercus petraea*, 18 Dec. 2011, A. Paz & C. Lavoise (LIP 0001138); isoeotype in herb. pers. A. Paz (IC18121102)* (Fig. 4.16).

Additional material studied. SPAIN, Cáceres, Jarandilla de la Vera, under *Quercus petraea*, 19 May 2012, A. Paz & C. Lavoise (IC19051231); ibid., 17 Dec. 2012, A. Paz & C. Lavoise (IC17121233); Cataluña, Girona, Susqueda, Mas la Jaça, under *Fagus sylvatica* and *Quercus pubescens*, 17 Sept. 2006, F. Rodríguez (JMV-20060917); ibid., 25 July 2013, F. Rodríguez (JMV-20130725); ibid., 11 Nov. 2013, F. Rodríguez (JMV-20131111).

Notes — The material kept in the Kew Herbarium (K(M) 162153) under the name '*Elaphomyces foetidus*' consists in half an ascocarp accompanied by a handwritten label '*Elaphomyces graveolens* Vitt.' handwritten by C. Vittadini, with a 'XI 12021' number added later. Although not dated, it is deducible that Vittadini sent this specimen to M.J. Berkeley before having published the definitive name *E. foetidus* (Vittadini 1842). The modern envelope is annotated 'Type of *Elaphomyces foetidus* Vittad', likely by D.N. Pegler. Another note was added by M.A. Castellano (4 Mar. 2009): '*Elaphomyces morrettii* Vittadini', a conclusion rejected here. This material is conspecific with other authentic collections (without detail on the labels) given by Vittadini to the Tulasne brothers as '*E. foetidus*' (PC, collections of Tulasne merged in the general herbarium), and partly returned to O. Mattiolo (part deposited at TO), which are constituted by sections of a large ascome, likely the complementary parts of the lectotype specimen at Kew.

The interesting evolution of the external spore wall (ornamentation) has been detailed in Paz et al. (2012). When mature, the high reticulum collapses and then requires minutia to be observed as it is; mature spores may appear smooth to a novice. Despite represented by a unique sequenced collection, this species can be unambiguously positioned as the sister clade of *E. cyanosporus*, from which it differs by 24 nts (Table 2).

Elaphomyces persoonii Vittad., Monogr. Tuberacearum: 70. 1831 — Fig. 4.17, 10e–f

Synonyms. *Lycoperdastrum persoonii* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Phlyctospora persoonii (Vittad.) Corda, Deutschl. Fl. III, 19: 22. 1841.

Lectotype (here designated MBT374423): iconotype, Vittadini, Monogr. Tuberacearum, pl. IV, f. 18. 1831 (only certified original material).

Epitype (here designated MBT374424): SPAIN, Cantabria, Monte Corona, *Castanea sativa*, *Quercus rubra* and *Fagus sylvatica*, 15 Feb. 2012, A. Paz & C. Lavoise (LIP 0001139); isoeotype in herb. pers. A. Paz (IC15021201)*.

Additional material studied. FRANCE, Bouteville, bois près Les Montendres, mixed forest, 4 May 2013, P. Chautrand (PCH13050301). — ITALY (?), s.loc., s.d., C. Vittadini (PC, herb. general ex herb. Tulasne, authentic material of *E. persoonii*) (Fig. 4.17); *ibid.* (TO, authentic material of *E. persoonii*, ex PC). — SPAIN, Cantabria, Monte Corona, under *Castanea sativa*, *Quercus rubra* and *Fagus sylvatica*, 18 Mar. 2012, A. Paz & C. Lavoise (IC18031201)*; Hazas de Soba, under *Castanea sativa*, 14 May 2005, A. Paz & C. Lavoise (IC14050509); Bielsa, under *Castanea sativa* and *Quercus robur*, 28 June 2008, A. Paz & C. Lavoise (IC28060836); Labarces, under *Castanea sativa* and *Fagus sylvatica*, 18 Apr. 2009, A. Paz & C. Lavoise (IC18040927); *ibid.*, 28 Feb. 2013, A. Paz & C. Lavoise (IC28021306); Rioturio, under *Quercus rubra* and *Castanea sativa*, 11 Jan. 2009, A. Paz & C. Lavoise (IC11010917).

Notes — See under *E. cyanosporus*.

Elaphomyces* sect. *Ceratogaster (Corda) Fr., Summa Veg. Scand. 2: 445. 1849

Holotype. *Elaphomyces maculatus* Vittad. (Corda 1841: 35).

Synonym. *Elaphomyces* sect. *Sclerodermei* (Vittad.) E. Fisch. in Engler & Prantl, Nat. Pflanzenfam. 1, 1: 312. 1897.

Notes — Vittadini (1831) divided the genus *Elaphomyces* into two unranked 'divisions': I. *Sclerodermei* and II. *Malacodermei*, *sine ordine*. The first was ranked as a subgenus by Clémencet (1932: 13). While Tulasne & Tulasne (1841) explicitly cited Vittadini's 'II. *Malacodermei*' (1831) as a section, we failed to find an equivalent combination of '*Sclerodermei*' prior to Fischer (1897b: 312).

Whether Fries (1849: 445) published the two subdivisions of *Elaphomyces* (*Ceraunium*, as '*Ceraunion*', and *Ceratogaster*) as unranked taxa, or as sections, as interpreted by Pfeiffer (1871–1873: 665; 1874–1875: 1178) and Dodge (1929), is debatable. According to Fries' (1849: 264) indications in the introduction of his opus, the second interpretation is adopted here. Would this not be accepted, the valid publication of sect. *Ceratogaster* should be attributed to Pfeiffer, but this would not affect the priority of sect. *Ceratogaster* over sect. *Sclerodermei* (Fischer 1897b).

Our exhaustive sampling of European *Elaphomyces* shows that 10 species with strong morphological affinities (Paz et al. 2012) form a robust monophyletic lineage (Fig. 2b). The combined ITS + 28S (Fig. 1) analysis confirms the distribution into two main clades suggested by the ITS analysis, splitting the European species into two groups, validated here as subsections: *E.* subsect. *Sclerodermei* (the *E. anthracinus*-group: *E. aculeatus*, *E. anthracinus* and *E. virgatosporus*), devoid of mycelial patches on the peridial surface, and *E.* subsect. *Maculati* (the *E. maculatus*-group: *E. leonis*, *E. leucosporus*, *E. leveillei*, *E. maculatus*, *E. moretii*, *E. septatus*, *E. spirosporus*) usually with yellow, greenish or purplish mycelial patches.

Elaphomyces* subsect. *Maculati Bellanger & P.-A. Moreau, subsect. nov. — MycoBank MB817255

Presence of yellow, greenish or purplish mycelial patches attached to the peridial surface.

Holotype. *Elaphomyces maculatus* Vittad.

Elaphomyces leonis P. Juste, F. García, J.M. Vidal & A. Paz in Paz et al., Bol. Micol. FAMCAL 7: 86. 2012 — Fig. 4.26, 11c–d

Material studied. SPAIN, Cantabria, Liébana, Fuente D, *Fagus sylvatica*, 23 Aug. 2015, A. Paz & C. Lavoise (IC23081504); Saja, under *Fagus sylvatica*, 13 Nov. 2011, A. Paz & C. Lavoise (IC13111101)*; *ibid.*, 14 Nov. 2011, A. Paz & C. Lavoise (IC14111101)*; *ibid.*, under *Fagus sylvatica*, 3 Jan. 2012, A. Paz & C. Lavoise (IC03011207); *ibid.*, 9 Sept. 2013, A. Paz & C. Lavoise (IC09091307); Segovia, Riofrío de Rianza, 15 Oct. 2001, A. Paz & C. Lavoise (LIP 0001146, holotype (Fig. 4.26); IC15100101 at AH and pers. herb. of A. Paz, isotypes); *ibid.*, under *Fagus sylvatica*, 13 Nov. 2011, F. García & P. Juste (IC131111–5).

Notes — The combined ITS + 28S phylogeny (Fig. 1) supports this species as basal to the inclusive clade encompassing *E. septatus*, *E. spirosporus* and *E. maculatus*, making *E. leonis* the best contemporary representative of the last common ancestor of this group of species.

Elaphomyces leucosporus Vittad., Monogr. Lycoperd.: 215. 1842. — Fig. 4.27, 11e–f

Synonym. *Lycoperdastrum leucosporum* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374440): iconotype, Vittadini, Monogr. Lycoperd., pl. III, f. 1. 1842 (only certified original material).

Epitype (here designated MBT374441): SPAIN, Asturias, San Esteban de Cuñaba, under *Castanea sativa*, 26 May 2012, A. Paz & C. Lavoise (LIP 0001147); isoeotype in herb. Pers. A. Paz (IC26051202)*.

Additional material studied. FRANCE, Ille-et-Vilaine, Aubigné, le Petit-Rond-Point, forêt domaniale d'Aulnay, mixed forest on rather thin rocky clay-limestone soil, 20 Oct. 2013, P. Chautrand (PCH13102001). — ITALY (?), s.loc., s.d., C. Vittadini (TO, authentic material of *E. leucosporus*) (Fig. 4.27); *ibid.*, comm. M.J. Berkeley (PC, herb. C. Montagne CM4390, authentic material of *E. leucosporus*). — SPAIN, Cantabria, Monte Corona, under *Fagus sylvatica*, 24 May 2012, A. Paz & C. Lavoise (IC24051203)*; *ibid.*, under *Quercus rubra* and *Fagus sylvatica*, 6 June 2011, A. Paz & C. Lavoise (IC06061117); Rioturbio, under *Fagus sylvatica*, 31 Mar. 2004, A. Paz & C. Lavoise (IC31030425); *ibid.*, 18 Mar. 2005, A. Paz & C. Lavoise (IC18030511); *ibid.*, under *Fagus sylvatica*, 27 July 2007, A. Paz & C. Lavoise (IC27070723); Hazas de Soba, under *Quercus petraea*, 15 May 2005, A. Paz & C. Lavoise (IC15050513); Uceda, under *Quercus robur*, 20 Apr. 2008, A. Paz & C. Lavoise (IC20040816); Bielsa, Labarces, under *Castanea sativa*, *Corylus avellana* and *Quercus robur*, 18 Apr. 2009, A. Paz & C. Lavoise (IC18040935).

Notes — Phylogenetically, this species is sister to *E. maculatus*, from which it differs by 10 nts (Table 2), a distance largely exceeding the D intra max of either species (0 nt, Table 2), but just below the barcode gap value of the genus (11.6 nts, Fig. 3). Because of the phylogenetic and morpho-anatomical vicinity of these two species and because *E. leucosporus* is nested in a clade of dark-spored species, it is tempting to speculate that this white-spored species represents a fixed albino of *E. maculatus* ancestor. Consistent with this hypothesis, *E. leucosporus* and *E. maculatus* display the same type or spore ornamentation.

Elaphomyces leveillei Tul. & C. Tul., Ann. Sci. Nat., Bot. Sér. II, 16: 21. 1841 — Fig. 4.28, 11g–h

Synonyms. *Elaphomyces maculatus* var. *leveillei* (Tul. & C. Tul.) Quél., Enchir. Fung.: 252. 1886.

Lycoperdastrum leveillei (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374442): FRANCE, Hauts-de-Seine, Meudon, spring or summer 1841, Tulasne (PC0167755, herb. C. Montagne CM4392, 2 ascomata) ('*Elaphomyces leveillei* Tul., in sylvis, Meudon prope Parisio, vere oc estate? (1841)') (Fig. 4.28).

Epitype (here designated MBT374443): SPAIN, Asturias, San Esteban de Cuñaba, under *Betula pendula*, 15 Mar. 2014, A. Paz & C. Lavoise (LIP 0001148); isoeotype in herb. pers. A. Paz (IC15031406)*.

Additional material studied. FRANCE, s.loc., 1869 (TO, coll. O. Mattirollo no. 69, 'autoptico' ex PC). — SPAIN, Asturias, San Esteban de Cuñaba, under *Betula pendula*, 26 July 2014, A. Paz & C. Lavoise (IC26071405); *ibid.*, 17 Nov. 2015, A. Paz & C. Lavoise (IC17111501).



Fig. 11 a–b. *Elaphomyces virgatosporus* (IC26051213). a. Ascomata; b. ascospores. — c–d. *Elaphomyces leonis* (IC13111101). c. Ascospores; d. ascomata. — e–f. *Elaphomyces leucosporus*. e. Ascomata (LIP 0001147, epitype); f. ascospores (TO, Vittadini). — g–h. *Elaphomyces leveillei*. g. Ascospores (PC 0167755, lectotype); h. ascomata (LIP 0001148, epitype). — Scale bars: a, d–e, h = 1 cm; b–c, f–g = 10 μ m. — Photos: a, d–e, h. C. Lavoise; b–c, f–g. A. Paz.

Notes — The Tulasne collections in PC, general herbarium, encompass numerous specimens of ‘crustae’ (mycelial crusts described by Tulasne & Tulasne 1841) dated 28 March, 15 April, 16 May, 23 May and 6 June 1841 from Meudon, but only two envelopes containing ascomata, likely original; one ‘in castaneis, 25 Apr. 1841’ is made of two intact ascocarps, but firmly stuck to the cardboard support and which could not be sampled for microscopy. It is preferred to designate as lectotype the well-preserved and fully annotated collection given by Tulasne to Montagne, kept in C. Montagne’s herbarium.

This species seems to be the only one in sect. *Ceratogaster* which is more abundant in Northern Europe (Tulasne & Tulasne 1841, Kers 1983) than in Spain or Italy, of which very few reports are known. It is also one of the very few widespread species not seen by Vittadini (1842).

Phylogenetically, the sister species of *E. leveillei* is *E. morettii*, the two species being separated by 24 nts (Table 2).

***Elaphomyces maculatus* Vittad., Monogr. Tuberacearum: 66. 1831 — Fig. 4.29, 12a–b**

Synonyms. *Ceratogaster maculatus* (Vittad.) Corda in Sturm et al., Deutschl. Fl. III, 19: 35. 1841.

Lycoperdastrum maculatum (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374444): iconotype, Vittadini, Monogr. Tuberacearum, pl. IV, f. 5. 1831 (only certified original material).

Epitype (here designated MBT374445): SPAIN, Cantabria, Cambilla, under *Corylus avellana* and *Fagus sylvatica*, 23 July 2011, A. Paz & C. Lavoise (LIP 0001149); isoeotype in herb. pers. A. Paz (IC23071103)*.

Additional material studied. ITALY (?), s.loc., s.d., C. Vittadini (PC0093930 ex herb. Tulasne, authentic material of *E. maculatus*); ibid. (PC, herb. C. Montagne CM4393, authentic material of *E. maculatus*) (Fig. 4.29); ibid., comm. M.J. Berkeley (PC, herb. C. Montagne CM4394, authentic material of *E. maculatus*). — NORWAY, Møre og Romsdal, Nesset, Eikesdal, Øvre Vike, in semi-rich deciduous forest under *Corylus avellana*, 16 Sept. 2011, T. Læssøe (AM36, O-F21188)*. — PORTUGAL, Guarda, Aguiar da Beira, *Pinus sylvestris*, 12 Nov. 2015, A. Paz & C. Lavoise (IC12111504). — SPAIN, Cádiz, El Cuartón, bosque de Niebla, *Quercus canariensis*, *Quercus pyrenaica* and *Quercus suber*, 27 Nov. 2015, A. Paz & C. Lavoise (IC27111501); Cantabria, Potes, under *Quercus petraea*, 11 June 2011, A. Paz & C. Lavoise (IC11061103)*; Linares, Pinerés, under *Quercus robur*, 11 Sept. 2008, A. Paz & C. Lavoise (IC11090805); Saja, Cambillas, under *Fagus sylvatica*, 27 Mar. 2005, A. Paz & C. Lavoise (IC27030534); ibid., under *Corylus avellana*, 11 July 2008, A. Paz & C. Lavoise (IC11070814); ibid., under *Fagus sylvatica*, 13 Sept. 2008, A. Paz & C. Lavoise (IC13090813); ibid., under *Corylus avellana*, 9 Nov. 2011, A. Paz & C. Lavoise (IC09111127); ibid., 1 Jan. 2014, A. Paz & C. Lavoise (IC01011401); Cahecho, under *Quercus suber*, 16 Jan. 2009, A. Paz & C. Lavoise (IC16010918); Palencia, Cervera, under *Fagus sylvatica* and *Corylus avellana*, 17 Apr. 2004, A. Paz & C. Lavoise (IC17040427).

Notes — The distribution of *E. maculatus* is here extended to Northern Europe. No macro- or microscopical difference was observed between this first Norwegian report and Southern collections. See also notes under *E. leucosporus*.

***Elaphomyces morettii* Vittad. var. *morettii* in Vittadini, Monogr. Tuberacearum: 71. 1831 — Fig. 4.30, 12c–d**

Synonyms. *Elaphomyces aculeatus* var. *morettii* (Vittad.) Qué., Enchir. Fung.: 253. 1886.

Lycoperdastrum morettii (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374446): iconotype, Vittadini, Monogr. Tuberacearum, pl. IV, f. 17. 1831. (only certified original material).

Epitype (here designated MBT374447): FRANCE, Moselle, Turquestein-Brancrupt, under *Pinus* sp., 14 Apr. 2013, J.-B. Pérez (LIP 0001150) (Fig. 4.30); isoeotype in herb. pers. A. Paz (IC14041302)*.

Additional material studied. ITALY, Lombardia, Rodero, 1902, O. Mattiolo (TO, coll. O. Mattiolo). — SPAIN, Asturias, Somiedo, under *Fagus sylvatica*, *Quercus* sp. and *Castanea sativa*, 1 June 2013, A. Paz & C. Lavoise (IC01061311).

Notes — No authentic material of *E. morettii* could be found in the herbaria K, PC and TO, but a collection from Vittadini exists in Fries’ collections at UPS. Most collections found deposited under this name by later authors are here assigned to *E. morettii* var. *echinatus*.

The phylogenetic analysis of this clade does not support *E. cantabricus* and *E. echinatus* as species distinct from *E. morettii* (Materials and Methods; Fig. 2b). However, these two taxa, distant from each other and from *E. morettii* by less than 5 nts, and with distinctive morphological features (Fig. 12), deserve the varietal rank (below and Table 2). See also notes under *E. leveillei*.

***Elaphomyces morettii* var. *cantabricus* (A. Paz & J.L. González) A. Paz & Lavoise, comb. & stat. nov. — MycoBank MB817256; Fig. 4.31, 13a–b**

Basionym. *Elaphomyces cantabricus* A. Paz & J.L. González, Butll. Assoc. Micol. Font i Quer 8: 4. 2008.

Material studied. HUNGARY, Keskemét, pine forest, 1907, L. Hollós (TO, as ‘*E. echinatus*’). — SPAIN, Asturias, Bayo, under *Castanea sativa*, 15 Aug. 1996, A. Suarez (ERD-1620); Iganzo, under *Castanea sativa*, 29 Mar. 2003, E. Rubio (ERD-3149); Arenas de Cabrales, under *Castanea sativa*, 5 Apr. 2003, J. Linde (ERD-5511); San Esteban de Cuñaba, under *Quercus robur*, 7 Feb. 2004, J. Linde (ERD-560); ibid., under *Castanea sativa*, 29 Apr. 2011, A. Paz & C. Lavoise (IC29041104)* (Fig. 4.31); Cantabria, Lamasón, *Castanea sativa* and *Quercus robur*, 2 June 2006, A. Paz & J.L. González (holotype AH36966; isotype APC2820); ibid., under *Castanea sativa* and *Quercus robur*, 19 Jan. 2007, A. Paz & J.L. González (APC2921); Bielsa, Labarces, under *Castanea sativa*, 21 Sept. 2006, A. Paz & J.L. González (APC2857); ibid., under *Castanea sativa* and *Quercus robur*, 28 June 2008, A. Paz (IC28060838); ibid., 18 Apr. 2009, A. Paz (IC18040914).

***Elaphomyces morettii* var. *echinatus* (Vittad.) Ceruti, Iconogr. Mycol. 28 Suppl. II: 10. 1960 — Fig. 4.32, 12e–f**

Basionym. *Elaphomyces echinatus* Vittad., Monogr. Lycoperd.: 81. 1842.

Synonym. *Lycoperdastrum echinatum* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374448): iconotype, Vittadini, Monogr. Lycoperd., pl. III, f. 1. 1842 (only certified original material).

= *Elaphomyces nucleatus* Sacc., Syll. Fung. 8: 870. 1889, invalid (McNeill et al. 2012, art. 36.1. Introduced by mistake by Saccardo 1889, as a synonym of *E. echinatus* Vitt.).

Material studied. FRANCE, Moselle, Turquestein-Blancrupt, Kiboki hotel, under *Pinus* sp., 27 May 2013, J.-B. Pérez (IC270513–7). — ITALY, Lombardia, Milano, May 1845, C. Vittadini (PC0093897 ex herb. Tulasne, authentic material of *E. echinatus*) (Fig. 4.32); Rodero, s.d., O. Mattiolo (TO, coll. O. Mattiolo, as ‘*E. echinatus*’); Trentino, val di Sole, s.d., G. Bresadola (TO, coll. O. Mattiolo as ‘*E. echinatus*’). — NORWAY, Vest-Agder, Kristiansand, under *Quercus* sp., *Picea abies* and *Betula pendula*, 27 Sept. 2013, A. Paz & C. Lavoise (IC27091306)*; ibid., moist forest under *Quercus robur*, *Tilia* sp., *Betula pendula* and *Picea abies* with *Vaccinium myrtillus*, 27 Sept. 2013, K. Hund, K. Killingmo & L. Hund (O-21292)*.

***Elaphomyces septatus* Vittad., Monogr. Tuberacearum: 67. 1831 — Fig. 4.33, 13c–d**

Synonym. *Lycoperdastrum septatum* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374449): iconotype, Vittadini, Monogr. Tuberacearum, pl. IV, f. 12c. 1831 (only certified original material).

Epitype (here designated MBT374450): SPAIN, Asturias, San Esteban de Cuñaba, under *Castanea sativa* and *Fagus sylvatica*, 13 May 2012, A. Paz & C. Lavoise (LIP 0001151); isoeotype in herb. pers. A. Paz (IC13051213)*.

Additional material studied. ITALY (?), s.loc., s.d. (TO, coll. O. Mattiolo) (Fig. 4.33). — SPAIN, Cantabria, Saja, under *Fagus sylvatica*, 8 Oct. 2006 (IC08100621)*; Asturias, San Esteban de Cuñaba, under *Castanea sativa* and *Fagus sylvatica*, 10 Apr. 2011, A. Paz & C. Lavoise (IC10041107)*; Cantabria, Aloños, under *Fagus sylvatica* and *Quercus robur*, 11 Oct. 2008, A. Paz & L. Barrio (IC11100819); Cambillas, under *Corylus avellana* and



Fig. 12 a–b. *Elaphomyces maculatus*. a. Ascospore (PC, Vittadini); b. ascomata (LIP 0001149, epitype). — c–d. *Elaphomyces moretii* var. *moretii*. c. Ascomata (LIP 0001150, epitype); d. ascospores (TO, Mattiolo). — e–f. *Elaphomyces moretii* var. *echinatus*. e. Ascospores (PC); f. ascomata (LIP 0001151, epitype). — Scale bars: a, d–e = 10 μ m; b–c, f = 1 cm. — Photos: a, d–e. A. Paz; b–c, f. C. Lavoise.



Fig. 13 a–b. *Elaphomyces moretii* var. *cantabricus* (IC29041104). a. Ascomata; b. ascospores. — c–d. *Elaphomyces septatus*. c. Ascomata (LIP 0001151, epitype); d. ascospores (TO, Vittadini). — e–f. *Elaphomyces spirosporus* (LIP 0001152, holotype). e. Ascomata; f. ascospores. — Scale bars: a, c, e = 1 cm; b, d, f = 10 µm. — Photos: a, c, e. C. Lavoise; b, d, f. A. Paz.



Fig. 14 a–f. *Elaphomyces roseolus*. a. Ascomata (LIP 0001143, holotype); b. ascospores; c. ascomata (JMV201409–16); d–f. details of the peridium. — g–h. *Elaphomyces aculeatus*. g. Ascospores (TO, Vittadini); h. ascomata (IC271115). — Scale bars: a, c, h = 1 cm; b, g = 10 µm; d–e = 20 µm; f = 1 mm. — Photos: a. G. Setkos; c. J.–M. Vidal; b, d–g. A. Paz; h. C. Lavoise.



Fig. 15 a–b. *Elaphomyces anthracinus* forma *anthracinus*. a. Ascomata (LIP 0001144, epitype), b. ascospores (PC, Vittadini). — c–j. *Elaphomyces anthracinus* forma *talosporus* (LIP 0001145, holotype). c. Details of gleba; d, f–h. ascospores; e, i–j. ascomata; f–j. ascospores. — Scale bars: a, e = 1 cm; b, d, f–h = 10 µm; c = 0.1 mm; i–j = 0.5 cm. — Photos: a, c, e, i–j. C. Lavoise; b, d, h. A. Paz.

Fagus sylvatica, 14 Aug. 2009, A. Paz & C. Lavoise (IC14080911); *ibid.*, 7 Nov. 2009, A. Paz & C. Lavoise (IC07110908); *ibid.*, 25 Sept. 2012, A. Paz & C. Lavoise (IC25091212); Liébana, Cahecho, under *Fagus sylvatica* and *Quercus petraea*, 5 Oct. 2012, A. Paz & C. Lavoise (IC05101211); Fuente D, *Fagus sylvatica*, 23 Aug. 2015, A. Paz & C. Lavoise (IC23081502); Málaga, El Palancar, *Quercus suber* and *Quercus canariensis*, 28 Nov. 2015, A. Paz & C. Lavoise (IC28111505); Soria, Cuevas de Agreda, under *Quercus faginea* and *Quercus ilex*, 23 Oct. 2015, A. Paz & C. Lavoise (IC23101502). — SWEDEN, Gotland, Mästerby änge, in deciduous forest under *Quercus* sp. and *Corylus avellana* on carbonated soil, 25 Sept. 2011, A. Molia & L. Hund (AM95, O-F21183)*.

Notes — Phylogenetically, the sister species of *E. septatus* is *E. spirosporus*, the distance between the two species (12 nts, Table 2) being just above the barcode gap of the genus (11.6 nts, Fig. 3).

Elaphomyces spirosporus A. Paz & Lavoise in Paz et al., Bol. Micol. FAMCAL 7: 89. 2012 — Fig. 4.34, 13e–f

Material studied. SPAIN, Cáceres, Jarandilla de la Vera, under *Quercus petraea*, 18 Dec. 2011, A. Paz & C. Lavoise (holotype LIP 0001152 (Fig. 4.34); IC18121101* in pers. herb. A. Paz, isotype); *ibid.*, 19 May 2012, A. Paz & C. Lavoise (IC19051208); *ibid.*, 19 Mar. 2013, A. Paz & C. Lavoise (IC19031319); Málaga, El Palancar, *Quercus suber* and *Quercus canariensis*, 28 Nov. 2015, A. Paz & C. Lavoise (IC28111506).

Notes — See under *E. septatus*.

Elaphomyces* subsect. *Sclerodermei (Vittad.) Bellanger & P.-A. Moreau, *stat. nov.* — MycoBank MB818576

Basionym. *Elaphomyces* [unranked] *Sclerodermei* Vittad., Monogr. Tuberacearum: 66. 1831.

Lectotype (here designated MBT374437): *Elaphomyces anthracinus* Vittad.

Notes — Vittadini (1831, 1842) did not provide any indication whether he considered ‘group a’ or ‘group b’ as more typical for his division *Sclerodermei*. Because *Elaphomyces anthracinus* is an uncritical species cited by Vittadini (1831) in his division *Sclerodermei* (group a) *Cortice laevi*, and matches adequately the short description: “*Cortex durus, fragilis, exsiccatione immutabilis. Sporidia majuscula*”, it is designated here as lectotype. Group b: *Cortice exasperato* encompasses species mostly found in the clade *Elaphomyces* s.str. (sect. *Elaphomyces*).

Elaphomyces aculeatus Vittad., Monogr. Tuberacearum: 70. 1831, illegit. (art. 52.1, see notes below) — Fig. 4.22, 14g–h

Synonym. *Lycoperdastrum aculeatum* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Elaphomyces rubescens R. Hesse, Hypog. Deutschl. 2: 75. 1894.

Material studied. FRANCE, Charente, Saint-Cybardeaux, les Bouchauds, Bois des Bouchauds, under *Quercus* sp., *Carpinus betulus* and *Corylus avellana*, 17 Sept. 2015, P. Chautrand (PCH15091702); Saint-Sornin, la Grande Mauvinière, *Quercus* sp., *Carpinus betulus* and *Corylus avellana* on clay-limestone soil, 22 Jan. 2013, P. Chautrand (IC17081303); *ibid.*, 17 Sept. 2013, P. Chautrand (PCH13012201). — HUNGARY, Kecskemét, oak forest, 15 Nov. 1907, L. Hollós (TO, coll. O. Mattirollo, as ‘*E. aculeatus*’) (Fig. 4.22). — ITALY (?), s.loc., s.d., C. Vittadini (PC, herb. C. Montagne CM4374, authentic material of *E. aculeatus*); *ibid.*, transmitted by M.J. Berkeley (PC, herb. C. Montagne CM4375, authentic material of *E. aculeatus*); *ibid.*, (K(M) 161169, herb. M.J. Berkeley). — SPAIN, Asturias, San Esteban de Cufiaba, under *Fagus sylvatica*, 27 Nov. 2011, A. Paz & C. Lavoise (IC27111115)*; *ibid.*, under *Fagus sylvatica* and *Castanea sativa*, 10 Apr. 2011, A. Paz & C. Lavoise (IC10041103)*; Cantabria, Cambillas, under *Corylus avellana* and *Fagus sylvatica*, 1 Feb. 2012, A. Paz & C. Lavoise (IC01021207); *ibid.*, 6 Sept. 2015, A. Paz & C. Lavoise (IC06091504); 20 Sept. 2015, A. Paz & C. Lavoise (IC20091513).

Notes — *Elaphomyces aculeatus* is illegitimate since Vittadini (1831: 70; 1842: 79) included *Lycoperdon scabrum* Willd., as interpreted by him (‘*saltem videtur*’) (McNeill et al. 2012, art.

52.1). In order to keep the use of this well-known and univocally interpreted name, a conservation proposal of *Elaphomyces aculeatus* with a *typus conservandus*, excluding the type of *L. scabrum* (Von Willdenow 1787: pl. 7, f. 19, a typical representation of *Elaphomyces muricatus* parasited by *Elaphocordyceps ophioglossoides* as already detected by Fischer 1897a: 103), will be the object of a forthcoming publication (in prep.).

Saccardo (1889: 870) cites as a synonym of *E. echinatus* an ‘*E. nucleatus*’ attributed to Tulasne & Tulasne (1841: 24) but this actually represents a formal mistake for ‘*E. aculeatus*’ cited by the French authors on the same page. This orthographic mistake ‘*nucleatus*’ is nevertheless erroneously registered in taxonomic databases such as Index Fungorum (www.index-fungorum.org) and MycoBank (www.mycobank.org), as a new name attributed to one of the Tulasne brothers.

Phylogenetically, the closest relative to *E. aculeatus* is *E. virgatosporus*, but the two sister clades are distant from 43 nts (Table 2), suggesting ancient radiation of these two taxa.

Elaphomyces anthracinus Vittad. **forma *anthracinus*** in Vittadini, Monogr. Tuberacearum: 66. 1831 — Fig. 4.23, 15a–b

Basionym. *Lycoperdastrum anthracinum* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374438): iconotype, Vittadini, Monogr. Tuberacearum, pl. III, f. 8. 1831 (only certified original material).

Epitype (here designated MBT374439): SPAIN, Cantabria, Torices, under *Quercus suber*, 31 Jan. 2009, A. Paz & C. Lavoise (LIP 0001144); isoeotype in herb. pers. A. Paz (IC31010903)*.

Synonyms. *Elaphomyces pyriformis* Vittad., Monogr. Lycoperd.: 72. 1842 (synonymy introduced by Fontana 1908).

Elaphomyces anthracinus var. *pyriformis* (Vittad.) Quél., Enchir. Fung.: 253. 1886.

Lycoperdastrum pyriforme (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891 (‘*pyriforme*’).

Elaphomyces plumbeus R. Hesse, Hypog. Deutschl. 2: 69. 1894.

Elaphomyces uliginosus R. Hesse, Hypog. Deutschl. 2: t. 22, f. 8. 1891 (see Kers 1981).

Additional material studied. ITALY, Lombardia, near Milano (‘recueilli près de Milan avec M. Vittadini dans une chênaie’, May 1849, C. Tulasne (PC0093872); Trentino, Trento, oak forest, 17 Mar. 1898, G. Bresadola (TO, as ‘*E. anthracinus* forma *pyriformis*’). S.loc., s.d., C. Vittadini (PC, herb. C. Montagne CM4378) (Fig. 4.23). — SPAIN, Cádiz, Los Barrios, Monte Mojeda Conejo, Carril de los Garlitos, *Quercus canariensis* and *Quercus suber*, 29 Nov. 2015, A. Paz & C. Lavoise (IC29111503); Monte Val de Infierno, mixed forest, 21 Nov. 2015, A. Paz & C. Lavoise (IC21111501); El Cuartón, Bosque de Niebla, *Quercus canariensis*, *Quercus pyrenaica* and *Quercus suber*, 25 Nov. 2015, A. Paz & C. Lavoise (IC25111504); San Roque, Pinar del Rey, mixed forest, 26 Nov. 2015, A. Paz & C. Lavoise (IC26111501); Cantabria, Bierva, under *Castanea sativa* and *Fagus sylvatica*, 18 Apr. 2009, A. Paz & C. Lavoise (IC18040937); Saja, under *Fagus sylvatica*, 9 Nov. 2011, A. Paz & C. Lavoise (IC09111103)*; *ibid.*, under *Fagus sylvatica*, 27 May 2012, A. Paz & C. Lavoise (IC27051212)*; *ibid.*, under *Fagus sylvatica* and *Corylus avellana*, 6 May 2009, A. Paz & C. Lavoise (IC06050930); Málaga, Cortes de la Frontera, La Calderona, *Quercus faginea* and *Quercus suber*, 24 Nov. 2015, A. Paz & C. Lavoise (24111503); El Palancar, *Quercus suber* and *Quercus canariensis*, 28 Nov. 2015, A. Paz & C. Lavoise (IC28111501); Palencia, Tosandes, under *Quercus ilex*, 17 Oct. 2010, A. Paz & C. Lavoise (IC17101003); Cervera, under *Fagus sylvatica*, 27 Feb. 2011, A. Paz & C. Lavoise (IC27021107).

Notes — In its current taxon sampling, the high ITS polymorphism of this clade (6 nts, Table 2) is driven by biogeography, the two Norwegian collections being separated from the Spanish ones by a well-supported short branch (Fig. 2b). However, no morpho-anatomical feature could so far be found to support naming a south European and a north European infraspecific taxa within *E. anthracinus*. Conversely, the collections cited below as forma *talosporus*, that is quite easily distinguished from typical *E. anthracinus* by several microscopical differences (see below), are not separated by ITS or 28S sequences and are thus proposed here at the formal rank.



Fig. 16 a–b. *Elaphomyces atropurpureus*. a. Ascomata (LIP 0001140, epitype); b. ascospores (PC, Vittadini). — c–d. *Elaphomyces citrinus*. c. Ascospores (PC, Vittadini); d. ascomata (LIP 0001141, epitype). — e–f. *Elaphomyces mutabilis*. e. Ascomata (LIP 0001142, epitype); f. ascospores (PC, Vittadini). — Scale bars: a, d–e = 1 cm; b–c, f = 10 μ m. — Photos: a, d–e. C. Lavoise; b–c, f. A. Paz.

Elaphomyces anthracinus* forma *talosporus A. Paz & Lavoise, *forma nov.* — MycoBank MB817254; Fig. 4.24, 15c–j

Differs from the type by globose-polyedric spores with six light faces, asci with 2–5 spores, and gradually darker peridium towards gleba.

Etymology. From Latin, *talus* = game dice, and *spora* = spore; refers to the cuboid shape of spores with rounded corners evoking 6-side dices.

Holotype. SPAIN, Asturias, San Esteban de Cufiaba, under *Castanea sativa* and *Fagus sylvatica*, 10 Apr. 2011, A. Paz & C. Lavoise (LIP 0001145); isotype in personal herbarium of A. Paz (IC10041104)* (Fig. 4.24).

Additional material studied. NORWAY, Oslo, Hovedøya, calcareous deciduous forest (*Corylus avellana*, *Tilia cordata*, *Quercus robur*, *Betula pendula* and *Pinus sylvestris*), 23 Sept. 2012, K. Hund, L. Hund, K. Killingmo & A. Molia (O-F245336)*; Buskerud, under *Pinus sylvestris* and *Corylus avellana*, 27 Oct. 2012, L. Hund & A. Molia (O-F245524). — SPAIN, Asturias, San Esteban de Cufiaba, under *Castanea sativa* and *Corylus avellana*, 26 May 2012, A. Paz & C. Lavoise (IC26051211)*; Cantabria, Saja, under *Corylus avellana*, 6 July 2008, A. Paz & C. Lavoise (IC06070803)*.

Elaphomyces virgatosporus Hollós, Ann. Hist.-Nat. Mus. Natl. Hung. 6: 318. 1908. — Fig. 4.25, 11a–b

Material studied. FRANCE, Jura, Porrentruy, sapinière de Bure, 20 Aug. 1879, L. Quélet (PC0093906, as '*E. echinatus*', ex herb. L. Quélet, PC); Meurthe-et-Moselle, Seney-aux-Forges, 28 Nov. 2011, J.-B. Pérez (IC281111–3). — NORWAY, Møre og Romsda, Nesset, 17 Sept. 2011, K. Hund, K. Killingmo, V. Hund & W.E. Johansen (AM62, O-F21180)*. — SPAIN, Asturias, San Esteban de Cufiaba, under *Castanea sativa* and *Corylus avellana*, 6 Mar. 2011, A. Paz & C. Lavoise (IC06031103)*; *ibid.*, under *Corylus avellana*, 26 Mar. 2011, A. Paz & C. Lavoise (IC26031101)*; *ibid.*, under *Corylus avellana*, 26 May 2012, A. Paz & C. Lavoise (IC26051213)* (Fig. 4.25); Cantabria, Saja, under *Corylus avellana*, 9 Aug. 2012, A. Paz & C. Lavoise (IC09081205); *ibid.*, 20 Sept. 2015, A. Paz & C. Lavoise (IC20091512).

Notes — See under *E. aculeatus*. This rarely observed species seems to be present all over Europe.

Elaphomyces* sect. *Malacodermei (Vittad.) Tul. & C. Tul., Ann. Sci. Nat., Bot., ser. 2, 16: 20. 1841 (*emend.*).

Lectotype (here designated MBT374425): *Elaphomyces mutabilis* Vittad.

Notes — Vittadini (1831) introduced the 'division' *Malacodermei* (without rank, first cited as section by Tulasne & Tulasne 1841, then as subgenus by Dodge 1929) for four species with a thin, smooth and soft surface and small spores: *E. papillatus*, *E. atropurpureus*, *E. mutabilis* and *E. citrinus*. This group, as defined by Vittadini, is clearly paraphyletic, and is revised here with exclusion of *E. papillatus* (sect. *Elaphomyces*), to match the ITS clade encompassing *E. atropurpureus*, *E. mutabilis*, *E. citrinus* and the novel *E. roseolus* species, with *E. mutabilis* proposed as lectotype for the section (Fig. 2c).

Elaphomyces atropurpureus Vittad., Monogr. Tuberacearum: 64. 1831 — Fig. 4.18, 16a–b

Synonym. *Lycoperdastrum atropurpureum* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374454): iconotype, Vittadini, Monogr. Tuberacearum, pl. VI, f. 1. 1831 (only certified original material).

Epitype (designated here MBT374455): SPAIN, Catalonia, Girona, Santa Coloma de Farnés, Sant Miquel de Cladells, 560 m, under *Quercus suber* on sandy substrate, 16 Sept. 2014, F. Rodríguez (LIP 0001140); isoeotype in herb. pers. A. Paz (JMV20140916–2)*.

Additional material studied. FRANCE, La Tremblade, Les Rouchards, Forêt de la Coubre, *Quercus robur* et *Pinus pinaster*, 13 Oct. 2015, P. Chautrand (PCH15101301). — ITALY, s.loc., May 1845, C. Vittadini (PC0093889, ex herb. Tulasne, authentic material, 2 packs) (Fig. 4.18). — SPAIN, Cáceres, Jarandilla de la Vera, under *Quercus petraea*, 16 Dec. 2012, A. Paz & C. Lavoise (IC16121201); *ibid.*, 19 Mar. 2013, A. Paz & C. Lavoise (IC19031317).

Notes — This rare and inconspicuous species (which forms the smallest cleistothecia in the genus) is remarkable by the purplish parietal pigment in the peridium. This species is very distant from its closest phylogenetic neighbours (68 nts, Table 2) and the numerous insertions present in its nuclear rDNA sequence suggest an ancient evolutionary origin. Its position in sect. *Malacodermei* is supported by the ITS analysis but unresolved in the rDNA combined analysis (Fig. 1, 2c).

Elaphomyces citrinus Vittad., Monogr. Tuberacearum: 65. 1831 — Fig. 4.19, 16c–d

Synonym. *Lycoperdastrum citrinum* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374433): iconotype, Vittadini, Monogr. Tuberacearum, pl. IV, f. 16. 1831 (only certified original material).

Epitype (here designated MBT374434): SPAIN, Cáceres, Jarandilla de la Vera, under *Quercus pyrenaica*, 18 Dec. 2011, A. Paz & C. Lavoise (LIP 0001141); isoeotype in herb. pers. A. Paz (IC18121104)*.

Additional material studied. ITALY, Lombardia, Milano, May 1845, C. Tulasne & C. Vittadini (PC ex herb. Roussel, authentic material); s.loc., s.d., C. Vittadini (PC, herb. C. Montagne CM4282, authentic material) (Fig. 4.19); *ibid.*, comm. M.J. Berkeley (PC, herb. C. Montagne CM4281, authentic material); Torino, Modero, winter 1898, Santini (TO, coll. O. Mattiolo). — SPAIN, Cáceres, Jarandilla de la Vera, under *Quercus pyrenaica* and *Q. petraea*, 19 May 2012, A. Paz & C. Lavoise (IC19051206).

Notes — The unique ITS sequence of this species generated for the present work is 100 % identical to that of a Spanish collection (MCVU16955) annotated '*E. citrinus*', indicating that this species displays no or limited polymorphism at the ITS locus (Fig. 2c). Conversely, *E. citrinus* displays one of the highest D inter min value of the whole dataset (48 nts, Table 2), suggesting that it has diverged from its closest known relatives *E. mutabilis* and *E. roseolus* early in the evolutionary history of the genus.

Elaphomyces mutabilis Vittad., Monogr. Tuberacearum: 65. 1831 — Fig. 4.20, 16e–f

Synonyms. *Lycoperdastrum mutabile* (Vittad.) Kuntze, Revis. Gen. Pl. 2: 858. 1891.

Lectotype (here designated MBT374435): iconotype, Vittadini, Monogr. Tuberacearum, pl. III, f. 12. 1831 (only certified original material).

Epitype (here designated MBT374436): SPAIN, Asturias, San Esteban de Cufiaba, under *Castanea sativa* and *Corylus avellana*, 27 Nov. 2011, A. Paz & C. Lavoise (LIP 0001142); isoeotype in herb. pers. A. Paz (IC27111103)*.

Elaphomyces mutabilis var. α *vittadini* Tul. & C. Tul., Fung. Hypog.: 103. 1851.

Elaphomyces mutabilis var. β *flocciger* Tul. & C. Tul., Fung. Hypog.: 103. 1851.

Elaphomyces mutabilis [unranked] *immutabilis* Speg., Michelia 1, 5: 469. 1879.

Elaphomyces mutabilis var. *immutabilis* (Speg.) Bataille, Bull. Soc. Mycol. France 36: 192. 1921.

Additional material studied. ITALY (?), s.loc., s.d., C. Vittadini (PC, herb. C. Montagne CM4395, authentic material of *E. mutabilis*) (Fig. 4.20). — SPAIN, Cádiz, El Cuartón, Bosque de Niebla, *Quercus canariensis*, *Quercus pyrenaica* and *Quercus suber*, 27 Nov. 2015, A. Paz & C. Lavoise (IC27111504); Cantabria, Monte Corona, under *Fagus sylvatica*, 3 Mar. 2012, A. Paz & C. Lavoise (IC03031201)*; *ibid.*, under *Fagus sylvatica*, 13 Mar. 2004, A. Paz & C. Lavoise (IC13030439); *ibid.*, under *Fagus sylvatica* and *Quercus rubra*, 28 Apr. 2005, A. Paz & C. Lavoise (IC28040525); *ibid.*, under *Pinus radiata* and *Abies alba*, 4 Sept. 2011, A. Paz & C. Lavoise (IC04091115); *ibid.*, 25 Sept. 2012, A. Paz & C. Lavoise (IC25091213); Hazas de Cestos, under *Castanea sativa*, 14 May 2005, A. Paz & C. Lavoise (IC14050523); Bárcena Mayor, under *Quercus robur*, 16 June 2007 (IC16060711); Uceda, under *Quercus robur*, 20 Apr. 2008, A. Paz & C. Lavoise (IC20040822); Bierva, under *Castanea sativa* and *Quercus robur*, 28 June 2008, A. Paz & C. Lavoise (IC28060836); *ibid.*, under *Corylus avellana* and *Fagus sylvatica*, 18 Apr. 2009, A. Paz & C. Lavoise (IC18040931); Rioturbio, under *Fagus sylvatica* and *Quercus rubra*, 11 June 2009, A. Paz & C. Lavoise (IC11060927).

Notes — Phylogenetically, *E. roseolus* displays sister-clade relationships with *E. mutabilis* (Fig. 2c), with one of the highest D inter min value of the whole genus though (52 nts, Table 2), revealing ancient splitting of these two species from their last common ancestor.

Elaphomyces roseolus Setkos, Kaounas, A. Paz, Lavoise & Fern. Rodr., *sp. nov.* — MycoBank MB817250; Fig. 4.21, 14a–f

Ascomata embedded in a pink-brown crust. *Peridial surface* grey-black, scrobiculate. *Peridium* cream white, slightly marbled with reddish tones. *Gleba* grey-black with purplish tinges. *Asci* globose, with 8 ascospores. *Ascospores* 9–11 µm diam, ornamented with thick rod-like warts of various height, forming a dense irregular perispore.

Etymology. *roseolus* = pinkish, referring to the characteristic colour of the mycelial crust embedding the ascomata.

Holotype. GREECE, Kastoria, mountains of Pierian, under *Carpinus orientalis* and *Juniperus* sp., 700 m elev., in acidic soil, 2 ascomata, 2 Oct. 2012, G. Setkos (LIP 0001143) (Fig. 4.21); isotype in the personal herbarium of A. Paz (IC02101201)*.

Ascomata globose to tuberiform, 30–60 mm diam, embedded in a pink-brown mycelial crust adhering to thin particles of sand and debris. *Peridial surface* grey-black, scrobiculate. *Peridium* thick 0.5–0.8 mm, cream white, slightly marbled by red tones. *Gleba* dark purplish brown. Smell weak. *Peridial surface* made of thick-walled cylindrical hyphae, septate, with grey-black pigment. *Peridium* made of very irregular hyphae, locally enlarged, thin-walled, arranged in alternated radially- and tangentially-oriented layers, more and more aggregated towards gleba and forming a thin layer of globose cells around gleba. *Asci* (only 2 observed) globose, 60–75 µm, 0.4–0.6 µm-thick walled, containing 8 spores. *Hyphae* of gleba cylindrical, 1.6–2.1 µm diam, colourless, thin-walled, abundantly branched. *Ascospores* sphaerical, 9–11 µm diam, ornamented with thick rod-shaped warts 0.5–1 µm high of unequal height, forming a compact perispore of irregular aspect.

Additional material studied. SPAIN, Catalonia, Girona, Santa Coloma de Farnés, Sant Miquel de Cladells, 560 m, under *Quercus suber* on sandy substrate, 16 Sept. 2014, F. Rodríguez (JMV20140916-1)*.

Notes — Macroscopically, the persistent mycelial crust of *E. roseolus* indicates affinities with *E. mutabilis*, *E. citrinus* and *E. atropurpureus*, forming sect. *Malacodermei*. The granulose surface of *E. mutabilis* and the nearly smooth surface of *E. atropurpureus* exclude the confusion with these species. *Elaphomyces citrinus* is the most similar by its scrobiculate peridium, but differs by the bright yellow mycelial crust. Microscopically, the ornamentation of spores is distinct from all above-cited species.

EXCLUDED SPECIES

Elaphomyces laevigatus F. Desp., Fl Sarthe: 452. 1838

Synonyms. *Melanogaster cauvinianus* Mont., Extr. Procès-Verbaux Séances Soc. Philom. Paris. 1844: 78 (illegit., Art. 53.1, superfluous new name for *E. laevigatus* F. Desp.).

Splanchnomyces cauvinianus (Mont.) Corda, Icon. Fungorum 6: 39. 1854 (illegit.).

Original material: unknown (no material located at PC).

Notes — The short description by Desportes (1838) is representative of a *Rhizopogon* (*Boletales*), based on a collection by Mrs Louise Renée Chauvin under pines ('bois de Funay', at Pontlieue, a locality now included to the city of Le Mans). In a series of oral communications presented at the monthly sessions of the Société Philomatique de Paris (published simultaneously; Anonymous 1844: 78, 88), Montagne indicates that he received

from Mrs Cauvin a collection made in Le Mans in October 1844, where the material seen by Desportes was collected. Montagne ('Séance du 16 novembre 1844'; Anonymous 1844: 78) first misinterpreted Desportes' publication as an erroneous report of *Rhizina laevigata* Fr., and proposed the new name *Melanogaster cauvinianus* Mont. based on material collected by Mrs Cauvin, with a detailed Latin diagnosis. One month later ('Séance du 14 décembre 1844'; Anonymous 1844: 88), Montagne recognized his mistake and justified retrospectively his new name *M. cauvinianus* by the inaccuracy of the epithet 'laevigatus' chosen by Desportes. Because the two reports were effectively published simultaneously, the second explicitly including the type of *E. laevigatus* in *Melanogaster cauvinianus* Mont., the later name must then be considered a validly published, but superfluous synonym of *Elaphomyces laevigatus* F. Desp.

The publication of the name *Splanchnomyces cauvinianus* by Corda (1854: 39), with a plate (t. II, f. 72) designated as lectotype by Martín (1996: 63), is explicitly based on the same material sent to Corda by Montagne, although Corda apparently ignored the already effective publication of Montagne's name as *Melanogaster*, cited 'in litteris'. We agree with Martín (1996) that the correct name for Mrs Cauvin's fungus is *Rhizopogon luteolus* Fr. & Nordh.

Elaphomyces pisi Tilak & Rokade, Mycopathologia 22: 340. 1964

Material studied. None.

Notes — This species described from India was revised by Patil et al. (2012), who found it to be a later synonym of *Rhopalostroma africanum* (Wakef.) D. Hawksw.

Elaphomyces sapidus Masee, Bull. Misc. Inform. Kew, 1910, 7: 252. 1910

Material studied. INDIA, s.loc.; United Provinces, Masee, 1910, hypogaeus, I.H. Burkill, K(M) 162157, lectotype (here designated).

Notes — The type of this species has been opportunistically placed among the *Scleroderma* collections at Kew (instead of its natural place in *Elaphomyces*), with a handwritten note by B.C. Zhang (21 Jan. 1988): "This collection is not a species of *Elaphomyces*. The author G. Masee's description do not agree with this specimen. I examined the specimen and found it is a *Basidiomycetes*. The clamp connection is visible in the hyphae from the dissepiments. According to the smooth surface, it is doubtful whether they are hypogaeal or epigaeal. Dr D.N. Pegler suggests it may be a species of *Scleroderma*. Further study needed". A second handwritten note of 'E.M. W.' states: "Thought this was type of *sapidus* Mass. — but does not answer to description". Michael A. Castellano (4 March 2009) also let a billet on the same envelope: "Not *Elaphomyces*. Apparently a *Scleroderma* sp.". Because Masee (1910) cited two collection numbers ('59, 518') after the collector (I.E. Burkill) and no other details, this material is not considered a holotype or isotype as indicated on the pack and is designated here as lectotype (MBT374451).

Microscopical observations: spores heavily ornamented by warts aggregated in crests, globose, 11 µm diam in average (including ornamentation). Rhizomorphs of pseudodimitic structure including broad pseudoskeletal hyphae, arising on surface as clusters of thick-walled, catenulate elements, 6.5–8.5 µm wide; generative hyphae 3.5–5 µm wide, pale yellow, smooth. Clamps present.

In our opinion the protologue (Masee 1910: 252) matches very satisfactorily this collection for macromorphology as well

as for spore size and ornamentation. The confusion between an *Elaphomyces* and a Basidiomycota can be explained by a deceptive morphology (basidiomata perfectly enclosed without trace of stipe, and rigid corky consistency).

Our morphological revision indicates that this material is a typical collection of an *Astraeus*. Some very similar species have been described recently from South-East Asia (Phosri et al. 2004, 2007, 2014), and one of them – the most similar being *Astraeus sirindhorniae* Watling et al. (in Phosri et al. 2014) – might be a later synonym of *E. sapidus*. Due to the lack of distinctive features on immature material and the still lacunar knowledge on Asian species of *Astraeus*, we refrain from proposing a synonymy with a currently defined species, but we aim to draw the attention of taxonomists to this forgotten name by introducing the new combination: *Astraeus sapidus* (Massee) P.-A. Moreau, *comb. nov.* (basionym. *Elaphomyces sapidus* Massee 1910, Bull. Misc. Inform. Kew 1910, 7: 252 – MycoBank MB817257).

The confusion between unopened *Astraeus* species and other genera such as *Scleroderma* is not recent. According to its original description, another species of *Astraeus* was described from Western China by Patouillard (1892) as *Phlyctospora maculata* Pat. The original material has not been revised so far.

Elaphomyces sulphureopallidus Vacek, Česká Mykol. 3, 3–5: 57. 1949

Material studied. CZECH REPUBLIC, Bohemia, Černosiče, 'in silva frondosa (*Carpinus*, *Quercus* etc.)', 23 Sept. 1947, V. Vacek (holotype PRM 673217), revised by J.M. Vidal.

Notes — The type material is represented by a single, globose fruiting body. Through the kindness of J.M. Vidal, who revised this specimen in 2002 and put his notes and pictures at our disposal, and after our own examination of a permanent slide kept by him, it can be affirmed that *E. sulphureopallidus* is a Basidiomycetes, with clamped peridial hyphae, septate capillitium and small spores measuring 7–12 µm diam, with reticulate ornamentation. These features fully correspond to those of an immature specimen of *Astraeus hygrometricus* (Pers.: Pers.) Morgan, following the most recent taxonomic treatment of the genus (Phosri et al. 2013).

Probably without having revised this collection, Szemere (1965) explicitly considered *E. sulphureopallidus* as a variety of *E. papillatus*, but did not formally validate the combination (McNeill et al. 2012, art. 35.2: incomplete reference to the basionym; see also Trappe 1969: 173, for a critical analysis of Szemere's work). Before reading J.M. Vidal's notes on the holotype, Szemere's interpretation was also ours, for a collection described above as *E. papillatus* var. *sulphureopallidus*, var. nov.

Elaphomyces trappei R. Galán & G. Moreno in Moreno et al., Mycotaxon 42: 206. 1991

Material studied. SPAIN, Extremadura, Badajoz, Lobón, under *Cistus ladanifer*, 8 May 1989, J. Espárrago, MA-Fungi 40577, isotype.

Notes — The description of *E. trappei* (Moreno et al. 1991) did not display characteristic features of the genus, especially because of the absence of a cleistothecial peridium, and were more characteristic of hypogeous *Pezizales*. The revision of the isotype of this species (by A.P. and C.L.) convinced us that *E. trappei* represents a species of *Terfezia*, for which we introduce the new combination:

Terfezia trappei (R. Galán & G. Moreno) A. Paz & Lavoise, *comb. nov.*

Basionym. *Elaphomyces trappei* R. Galán & G. Moreno in Moreno et al., Mycotaxon 42: 206. 1991, MycoBank MB821518).

Synonym. *Terfezia cistophila* Ant. Rodr. et al. (in Bordallo et al. 2015: 245) is a later synonym.

DISCUSSION

Species limits and ITS barcoding in Elaphomyces

Defining species limits in Fungi, which do not lend themselves easily to cultivation, remains a challenging issue for phylogeneticists and constitutes a major subject of debate with field taxonomists, who rely on morphological, anatomical, sometimes also ecological, characters of fruit bodies to diagnose supposedly biological species. Here we provided the first comprehensive overview of European *Elaphomyces* based on a combined approach of morphological and molecular data. Genealogical concordance in phylogenetic species recognition (GCPSR) and DNA barcoding methods have been developed to circumscribe evolutionary species, although none of the two methods can identify the moment that individuals in an ancestral species are split into progeny species (Taylor et al. 2000, Giraud et al. 2008, Seifert 2009, Schoch et al. 2012, Osmundson et al. 2013, Garnica et al. 2016).

As defined here, *Elaphomyces* species are primarily phylogenetic units, amenable to ITS DNA barcoding when considering intraspecific and interspecific phylogenetic distances within pairs of sister clades. However, following a genus-wide barcoding approach would lead to define species limits at 11.6 nucleotide differences, which represents 1.7 % of an average 700 base pairs ITS sequence. Such a barcode gap value is in the range of that observed in other fungal taxonomic groups (Frøslev et al. 2007, Jargeat et al. 2010, Osmundson et al. 2013, Bellanger et al. 2015, Garnica et al. 2016), but applied as a threshold, it would fail to resolve 20 % (5/25) of species that nonetheless fulfil our phylogenetic criteria. As already pointed out, such method often fails at resolving closely related species that did not have time to accumulate enough differences since splitting from their last common ancestor (Du et al. 2012, Kiss 2012, Schoch et al. 2012, Garnica et al. 2016).

Spore characters in Elaphomyces

At the same time as he revealed the diversity of *Elaphomyces* species in Europe, Vittadini (1831) enlightened the importance of spore characters for the recognition of each species. Spores have been used by all following authors as the most significant specific features. Spore sizes are useful to characterise some remarkable species (*E. roseolus* and *E. mutabilis* with the smallest spores, 9–11 µm wide, or *E. maculatus* with the largest, up to 42 µm wide); more generally the smallest spores (less than 16 µm wide) are found in the basal lineages *Ascoscleroderma* and *Malacodermei* (Table 3). Colours characterise some other outstanding species: *E. cyanosporus* is unique in Europe by the bluish spore content, but the spores are usually coloured by a yellow-brown or black pigment concentrated in the exospore (ornamented layer), and thus also depends on the development of the exospore. Some unpigmented collections are reported above in *E. granulatus* (forma *pallidosporus*, and '*E. leucocarpus*' as an immature stage) and *E. papillatus* (forma *sulphureopallidus*), in which the ornamentation is normally developed but devoid of pigment. In *E. mutabilis* a high proportion of unpigmented (immature?) spores is always observable among normally coloured ones. The case of *E. leucosporus* is singular, as this well-defined species with white spores (actually with only partially coloured exospores; Fig. 11f) belongs to a lineage of dark-coloured species (sect. *Ceratogaster*) of

Southern Norway (Oslo area) that concentrates this diversity. However, this contrasted pattern among European regions should be considered with caution as it also reflects the uneven geographical distribution of mycological investigations during the last century. Interestingly, these areas are characterised by a mild oceanic climate, with abundant precipitations, in a granitic geological context. Most species seem to have a pan-European distribution, although northern Europe seems to be less diversified in general; only *E. asperulus* and *E. leveillei* seem to be somewhat more common in Northern areas than in Italy or Spain. The occurrence of even rather rare species such as *E. papillatus*, *E. maculatus*, *E. quercicola* from Poland (Ławrynowicz 1988) to western Spain, or *E. virgatosporus* from Hungary to Norway and Spain (Læssøe et al. 2009) suggest that most species can be found throughout Europe, and probably including more eastern areas where hypogeous fungi have been less investigated in general.

Exceptions are the most common and widespread species *E. decipiens*, *E. granulatus*, *E. muricatus*, which are found in association with most EcM tree species (including exotic tree species such as *Pinus radiata* and *Eucalyptus* spp.) and across a wide range of soil conditions. Interestingly, the three broad host-range species are all also known from North America. Only a few exceptions seem to display clear host preferences. Narrow-host range species are scattered across *Elaphomyces* phylogeny as follows. First, in sect. *Ceratogaster*, the Northern species *E. leveillei* was only found in *Betula* spp. forest stands. Second, in sect. *Ascoscleroderma* all fruiting reports of *E. persoonii* were from *Castanea sativa* dominated stands (although other possible host trees were usually present). Similarly, the four species which associate with both Gymno- and Angiosperms, namely *E. anthracinus*, *E. asperulus*, *E. moretii* and *E. mutabilis*, are dispersed in all sections. Interestingly, and similarly to other ectomycorrhizal ascomycetes (Taschen et al. 2015), potential interaction between *Elaphomyces* and endomycorrhizal plant species may occur during the biological cycle of the fungus, as fruiting patterns have been repeatedly mentioned under the endomycorrhizal *Rosaceae* *Crateagus monogyna* (*E. granulatus*, *E. muricatus*, *E. cyanosporus*) and the *Cupressaceae* *Juniperus* sp. (*E. roseolus*). Understanding the nature of the interaction between endomycorrhizal plants (e.g. direct vs indirect, micro-environmental vs biotic) and these *Elaphomyces* species would help to provide a comprehensive overview of their ecology.

Similarly, soil pH requirements widely vary depending on *Elaphomyces* species. Most species also display a clear affinity for acidic soils. Contrastingly, six species (i.e., *E. aculeatus*, *E. barrioi*, *E. leonis*, *E. leveillei*, *E. moretii*, *E. septatus*) tolerate neutral soil pH, and three of them (i.e., *E. anthracinus*, *E. cyanosporus* and *E. violaceoniger*) have been recorded on carbonated soils. *Elaphomyces violaceoniger* is only known from *Quercus* forests on limestone, while *E. cyanosporus* has been reported from walls of chalk quarries (Clowez et al. 2015).

The phenology of *Elaphomyces* species is rarely analysed in literature. However, contrasted phenology exists. If most species seem to be observable all over the year, with a fruiting peak from March to November, some of them show marked preference for ascocarp production in spring (*E. leucosporus*), summer (*E. persoonii*) and winter (*E. spirosporus* and *E. cyanosporus* which fruit from November to March).

Towards an infrageneric classification of *Elaphomyces*

Thanks to the first molecular assessments of the genus by Reynolds (2011) and Castellano et al. (2016), mainly based on North American and tropical species, the combined rDNA analysis proposed here (Fig. 1) with the inclusion of most European species, provides a rather robust phylogenetic reconstruction

of the genus, which is interpretable with regards to our current knowledge of the morphology of the species.

Section *Ascoscleroderma*

The taxonomic isolation of reticulate-spored species of *Elaphomyces* is not a new idea. Corda (1841) segregated them in the genus *Phlyctospora*, originally based on *P. fuscum* (1841: 51; now a *Scleroderma*, see, e.g., Guzmán et al. 1970), but including *E. persoonii* (Corda 1841: 22). This assimilation was already contested by Tulasne & Tulasne (1851: 112) and stirred the anger of Mattiolo (1903: 348), who accused the last authors to have invented Corda's combination of *P. persoonii*.

With more moderation, Fischer (1897a: 99) separated *E. cyanosporus*, *E. foetidus* and *E. persoonii*, as a division of '*Sclerodermei*', from *E. variegatus* and allies, by ascomata with more distinct base and glabrous surface. This division was erected as a genus by Clémencet (1932) based on the same character, who introduced the new name *Ascoscleroderma*. Although rejected by ancient and modern authors (e.g., Tulasne & Tulasne 1851, Hawker 1954), *Ascoscleroderma* is shown here to represent one of the most basal lineages (Fig. 1), but its relationships with sect. *Malacodermei* and with the *Pseudotulostoma* clade are not yet resolved. However, the relativeness of the stalked species *Pseudotulostoma volvata* already identified by Reynolds (2011), and recently enriched by other Amazonian species by Castellano et al. (2016), suggests that the tendency to form a more or less developed base or pseudostipe might be a common feature of the most archaic species in the genus. Also, spore ornamentations in these taxa are distinct from all other *Elaphomyces* species and incites to interpret the low, more or less complete reticulum as a plesiomorphic character.

Section *Ascoscleroderma* is here defined as to encompass all species with low reticulate to labyrinthiform spores and devoid of mycelial coating. As suggested in Fig. 2c, it includes a 'Eurasian lineage' including *E. cyanosporus*, *E. foetidus* and *E. persoonii*, and an 'Amazonian lineage' (Castellano et al. 2012c, 2016; Fig. 1) including *E. compleximurus*, *E. favosus* and *E. labyrinthicus*. This apparent biogeographic disjunction may obviously result from insufficient sampling in other regions, especially Eastern and Central Asia, but also North America. None of the Australian or East Asian species described without molecular data by Corner & Hawker (1953), Imai (1960) or Castellano et al. (2011) seem to belong in this section.

However, several species should be investigated further: *E. reticulosporus* from China (Zhang 1991) and the provisionally named *E. 'novae-zelandae'* of Castellano et al. (2011) and '*E. fallax* Castellano & Trappe', ined. (introduced by Beug et al. 2014: 80) from North America and recently validated as *E. oreoides* Castellano by Castellano & Stephens (2017), are all apparently related to *E. persoonii* and *E. cyanosporus*.

The position of *Pseudotulostoma volvatum* and *P. japonicum* and their *Elaphomyces*-like relative *E. adamizans* is discussed – but not solved – by Reynolds (2011) and Castellano et al. (2016). If molecular data do not support the inclusion of this group within sect. *Ascoscleroderma* (Fig. 1), subreticulate spores as well as presence of a more or less developed pseudostipe (evoked above in *E. cyanosporus*; Clémencet 1932) argues in favour of this inclusion. Following Castellano et al. (2016), we will not propose any new combination for these species insufficiently known to us, although they will be obviously necessary in the perspective of a worldwide systematics of the genus.

Section *Elaphomyces*

The autonymic section including the type species *E. cervinus* (see Notes under *E. granulatus*) is the most documented in

genetic databases, essentially because of the abundance of concerned species in ectomycorrhizae of temperate and sub-arctic forests. It is also the latest lineage, as suggested by short interspecific phylogenetic distances as well as the relatively soft morphological divergences between the species described here. With the exception of the European *E. papillatus* with its distinctive striate spores (the Asian *E. porcatosporus* and the Australian *E. suejoyceae* seem to be the only extra-European related species described so far; Zhang 1991, Castellano et al. 2011), all species in this section display spores with a thick exospore made of yellow-brown hairs, of which the patterns of aggregation is the main specific character interpretable in taxonomy. Macromorphological features include the structure, aspect and development of peridium warts, heterogeneity of endoperidium, presence of a separable or incrusting mycelial coating, and colours of each element of peridium, with some inconstant features such as occasional blue tinges in *E. asperulus*.

The *E. muricatus* and *E. granulatus* lineages display a holarctic distribution, with some transcontinental species present across Europe and North America (*E. asperulus*, *E. decipiens*, *E. granulatus*, *E. muricatus*) and a small lineage of rare species split into European (*E. barrioi*) and West American species (*E. 'decipiens' ss. Trappe*, representing two lineages). More species have been described in literature without molecular data and can only be suspected to belong to this section at now, but it is already attested by DNA sequences that at least one Indonesian, one African and one Australian species belong to the *E. granulatus*-group (species 5, 7 and 8 of Castellano et al. 2016: f. 1). According to the original descriptions, it is likely that at least *E. japonicus* (Lloyd 1916), *E. shimizuensis* and *E. neosasperulus* (Imai 1960), *E. subvariegatus* (Imai 1935) and *E. asahimontanus* (Sato et al. 2010) from Japan, *E. putridus* (Castellano et al. 2012a) from New Zealand, *E. austrogranulatus* and *E. aurantius* (Castellano et al. 2011) from Australia, and *E. spinoreticulatus* (Zhang & Minter 1989) and *E. americanus* Castellano and *E. remickii* Castellano & R.B. Stephens (Castellano & Stephens 2017, the first already introduced as '*E. americanum* Castellano & Trappe, ined.' by Beug et al. 2014: 78) from North America, belong in these *E. granulatus*/*E. muricatus* groups (or subsections *Elaphomyces* and *Muricati*).

Finally, the Japanese *E. fragilisporus* (Imai 1939–1940) and the Floridean *E. verruculosus*, with gigantic (30–40 and 35–46 µm wide, respectively) and punctuate-striate spores (Castellano et al. 2012b, Beug et al. 2014: 82), and nearly smooth exoperidium, are suspected to be related to *E. papillatus*. They might as well represent another distinct clade in this section. Also, *E. suejoyceae*, described with large ascomata from Australia, could be close to these species but in this case the spores are smaller, 26–30 µm (Castellano et al. 2011).

Section *Malacodermei*

This section is defined in Europe by four species, all highly distinct but with a characteristic mycelial coating and small spores with low labyrinthiform ornamentation: *E. atropurpureus*, *E. citrinus*, *E. mutabilis* and *E. roseolus*. This diversity, as well as the long genetic distances between them, illustrate a long-time divergence congruent with their basal phylogenetic position (Fig. 1) and the Gondwanian origin of the genus (Castellano et al. 2016). Outside this section, a mycelial coating is also found in *E. aculeatus* (sect. *Ceratogaster*), but this coating is of different nature, thinner and with larger spores (12–15 µm in average and with a more developed exospore).

Although no extra-European sequence is available in public databases, morphological descriptions of so far molecularly undocumented species suggest that this group is much more

diversified worldwide, and especially in SE Asia and Australia. For instance, species with bright yellow or lemon-yellow (*E. bollardii*, *E. luteicrustus*, *E. chlorocarpus*, *E. pedicularis* from Australia and New Zealand, Castellano et al. 2011, 2012a; *E. viridisepium* from North America, Trappe & Kimbrough 1972) or pinkish to purplish mycelium (*E. nikkoensis* from Japan, Imai 1938; *E. singaporensis* from Singapore, Corner & Hawker 1953; *E. appalachiensis* from North America, Linder 1939, Castellano et al. 2012b), should find their natural place in sect. *Malacodermei*.

Section *Ceratogaster*

This section encompasses mostly dark-coloured species with smooth to weakly warty peridium, and medium- to very large spores. The spore ornamentation is remarkably diverse, without clear pattern in comparison with the phylogenetic reconstructions of the lineage. The distribution of European species into two subsections (subsect. *Maculati* and *Sclerogaster*) is not easily interpreted through morphological features, and the diversity in Europe (with 10 species recognized here; Fig. 2b) might also be observed at least in North America and Asia. Actually, only the East Asian species *E. guangdongensis* and the African species *E. iupperticellus* (Fig. 1), both with striate spores, are molecularly documented outside Europe so far (Castellano et al. 2016). Buyck et al. (2016) also identify from a single ITS phylogeny an '*E. guangdongensis* clade' encompassing *E. guangdongensis* and three representatives of subsect. *Maculati*. The addition of extra-European sequences and the inclusion of 28S locus, in addition to ITS, is necessary to interpret the evolutionary significance of morphological features in such an early-diverging lineage.

Only a few descriptions seem to concern extra-European species with large spores, dark colours and weakly verrucose peridium. In Asia, the list is limited to *E. miyabeanus* and *E. nikkoensis* from Japan (Imai 1929, 1938), both being the hosts of the parasitic '*Cordyceps*' *jezoensis* (Reynolds 2011). In North America, Castellano & Stephens (2017) recently validated two new species in this section: *E. bartlettii* Castellano & R.B. Stephens and *E. macrosporus* Castellano & T.S. Elliott, both related to *E. leveillei*. A third species is illustrated by Beug et al. (2014: 80) as '*E. loebae* Castellano, nom. prov.').

SYSTEMATIC KEY TO EUROPEAN SPECIES OF ELAPHOMYCES

Key to sections

1. Ascomata embedded in a dense mycelial coating, yellow, white, purplish or pinkish sect. *Malacodermei*
1. Ascomata without mycelial coating, at most with sparse rests of white, cream, yellow or greenish mycelium 2
2. Peridial surface yellow- to brownish coloured, with warts yellow, light brown to cinnamon brown sect. *Elaphomyces*
2. Peridial surface dark-coloured, smooth or with black to dark reddish brown 3
3. Spores reticulate at least before maturity, sometimes very faintly verrucose when mature sect. *Ascocladerma*
3. Spores warty-spiny with isolated spines, sometimes catenulate or arranged in crests or spirals sect. *Ceratogaster*

Section *Elaphomyces*

1. Spores cretate. Cortex of ascomata papillate or areolate. Ascomata 5–30 mm diam (subsect. *Papillati*) *E. papillatus*

Varieties:

- cortex ochre-yellow to chestnut brown, with dark areoles forming a net-like ornamentation. Peridium 2–3 mm thick,

- bluish grey with brown veins. Spores (11–)12–15(–16) μm diam, with 1–2 μm high crests branched, short and interwoven. — Southern Europe. var. *papillatus*
- cortex nearly smooth, with small dark areoles; peridium 1.5–2 mm thick, bluish grey; spores almost hyaline, 13–16 μm diam. — Central and Southern Europe var. *sulphureopallidus*
- ascomata smaller < 10 mm diam, with rests of yellow mycelium, on cortex with flat black warts on reddish ground; spores (12–)14–17(–19) μm with crests 2–3 μm high, long and parallel. — Scandinavia var. *striatosporus*
1. Spores echinulate. Cortex of ascomata with protruding, flattened or granular warts 2
 2. Inner peridium marbled or spotted in cross-section (subsect. *Muricati*). 3
 2. Inner peridium not marbled in cross-section (subsect. *Elaphomyces*). 7
 3. Peridium in cross-section dark purple-brown marbled by cream white radial veins. Ascomata 10–50 mm wide, with adpressed cream white mycelium remnants. Cortex with flat warts, dark grey-brown on lighter ground. Gleba reddish grey-brown to black. Spores 19–26 μm diam with short thin rod-like warts aggregated in thin isolated meshes *E. decipiens*
 3. Peridium in cross-section with circular or elliptical dots. . . 4
 4. Peridial surface with large acute warts, with mycelial cords and debris strongly adherent. Ascomata large, 10–50 mm wide. Peridium 2–5 mm thick, marbled (granular aspect), dark, vinaceous towards gleba. Spores 19–25 μm wide, rod-like warts isolated, thick and curved . . . *E. quercicola*
 4. Peridial surface with very unequally prominent warts, easily released from debris and mycelium 5
 5. Inner peridium white in cross-section, marbled with circular or ellipsoidal dots *E. muricatus*
- Varieties:
- ascomata 10–30 mm diam, peridial warts small, peridium 1–3 mm thick, dark with white veins, spores (16–)18–21(–23) μm with thin curved rod-like spines forming loops var. *muricatus*
- ascomata 10–50 mm diam, with basal depression, peridium 2–5 mm thick, lighter-coloured, spores 15–20 μm with thick rod-like spines forming irregular meshes. . . var. *variegatus*
- ascomata 10–30 mm diam, with low hardly distinct warts, peridium thin marbled, light at first and darkening when drying, with regular veins, spores 19–28 μm . var. *reticulatus*
5. Inner peridium vinaceous in cross-section, marbled with ellipsoidal dots 6
 6. Peridial surface with prominent warts, light yellow-brown. Spores 19–24 μm , with thick rod-like spines strongly curved and short, confluent at apex and forming irregular meshes *E. barrioi*
 6. Peridial surface with prominent warts, light brown. Spores 22–24 μm , with rod-like spines confluent and drawing plaits *E. violaceoniger*
 7. Peridium white to yellowish *E. granulatus*
- Forms:
- ascomata irregular, 15–80 mm diam. Peridial surface with granular warts. Peridium smooth, white to yellowish. Gleba brown, reddish to black when mature. Spores 20–29 μm , with rod-like warts 2 μm high, very thick, confluent at apex forma *granulatus*
- ascomata irregular, 15–50 mm. Peridial surface with flat irregular warts. Peridium smooth, cream white. Gleba light pinkish when mature. Spores 20–28 μm , almost hyaline forma *pallidosporus*

7. Inner peridium white, often with bluish tones at first then with vinaceous tinges 8
8. Peridial surface with densely arranged granular warts, on a granular peridium. Warts light greyish brown. Spores 23–28 μm , with rod-like warts 1–2 μm high, crowded and forming a granular perisporium. *E. hassiacus*
8. Peridial surface with flat warts forming scales of various colours and depressions forming a net-like surface. Spores 22–30 μm , with short rod-like warts randomly arranged, forming a patched perisporium *E. asperulus*

Section *Ascocladerma*

1. Spores 26–32 μm , with a high reticulum 4.5–5 μm thick, of small alveoles 1.5–2 μm broad at first, collapsing and appearing minutely verrucose when mature. Ascomata globose, 20–45 mm diam, irregular, without conspicuous base, without remnants of yellow mycelium. Cortex dark grey-blue, with very irregular granular warts, each one surrounded by a depression. Gleba bluish grey (young), surrounded by a grey-white persistent membrane. Smell strong, of ricin oil *E. foetidus*
1. Spores smaller, persistently reticulate with broad alveoles > 2 μm wide, still distinct at maturity 2
2. Spores 18–22 μm , with reticulum 2.5–3.5 μm thick, alveoles double-walled 3–4 μm wide, very irregular. Ascomata large, 30–70 mm diam. Cortex with prominent warts, with strongly adherent yellow mycelial cords. Peridium 2–4 mm thick, grey-white, darker towards gleba. Gleba bluish green *E. persoonii*
2. Spores 23–26 μm , with reticulum 1.5–2.5 μm thick, alveoles simple-walled 2–3.5 μm wide, regular. Ascomata smaller, 15–30 mm diam, with a mycelial base. Cortex with hardly prominent and irregular warts. Peridium thick, double-layered, the outer layer white with reddish tones, the inner layer forming a dark halo around the gleba. Gleba grey-blue, with intense smell of *Tuber* *E. cyanosporus*

Section *Ceratogaster*

1. Peridial surface purple to purplish red with protruding warts black inside, purplish at apex under the soil coating. Peridium thick, whitish. Spores (13–)15–18(–20) μm diam with thin rod-like warts confluent at apex and forming folds *E. aculeatus*
1. Ascomata without purple mycelial coating. 2
2. Ascomata with greenish mycelium adhering to the surface 3
2. Ascomata without greenish mycelium 4
3. Spores large, 28–42 μm diam, with thin very crowded rod-like warts of various height, giving a compact, irregular appearance. Ascomata large, 20–50 mm diam. Peridial surface black, slightly striate under lens, with persistent green spots and surrounded by green mycelium. Peridium thick, white *E. maculatus*
3. Spores 18–25 μm , with thick rod-like warts 1.2–1.8 μm high, randomly confluent and forming a fragmented perisporium. Ascomata globose with at least one flattened side, usually with several depressions. Peridial surface black, with small dark brown warts visible under lens. Peridium thick, greyish white *E. leveillei*
4. Peridial surface smooth to slightly papillate. 5
4. Peridial surface distinctly verrucose 9
5. Spores pale, yellow to cinnamon brown 6
5. Spores dark, reddish brown to black 8

6. Ascomata 20–40 mm diam, dark grey-brown, rough with small craters, without green mycelial meshes. Peridium thick, pinkish white. Gleba when fully mature cream with pinkish tones. Spores 28–32 µm, with rod-like warts 3 µm high, irregular, forming a compact and rough perisporium *E. septatus*
6. Ascomata smaller, 5–15 mm diam. Spores smaller 7
7. Spores with thick rod-like warts of irregular height forming a rough and waved perisporium. Ascomata with basal cavity, embedded in a green and purplish mycelium. Peridial surface dark grey-brown, almost smooth. Peridium thick, greyish brown. Gleba when fully mature light coffee-brown. Spores 18–22 µm *E. leucosporus*
7. Spores with very short rod-like warts longitudinally aligned, forming spirals. Ascomata with basal cavity and protuberances, embedded in a greenish mycelium. Peridial surface dark brown. Peridium light pinkish grey. Gleba cinnamon-brown with greyish tones. Spores 18–23 µm *E. spirosporus* (if warts with yellow content in cross-section, see *E. papillatus* forma *striatosporus*, in sect. *Elaphomyces*)
8. Peridium thick, young light coffee-brown, darkening with age. Spores 22–28 µm, with thin rod-like warts 2 µm high, confluent and forming a fragmented perisporium. Ascomata 15–30 mm diam, globose to irregular, with protuberances. Peridial surface minutely granular, dark grey-brown with red and blue tinges *E. leonis*
8. Peridium thick, white or pale yellowish contrasting with the dark gleba, with intense smell. Spores 15–20 µm, with thick isolates rod-like warts confluent at apex and forming a dark brown to black perisporium of verrucose aspect. Ascomata irregular, blackish brown, with characteristic intense smell. Peridial surface slightly granulose under lens, hard and charcoal-like. Peridium thick, yellowish white. Gleba very dark, almost black *E. anthracinus*

Forms:

- spores globose, uniformly coloured ... forma *anthracinus*
- spores dodecagonal with lighter sides, ascomata with small umbo and slight basal cavity forma *talosporus*
- 9. Spores 16–22 µm, with perisporium arranged in parallel and waved crests. Ascomata 14–26 mm diam, embedded in a dense coating of substrate and reddish brown mycelial cords. Cortex dark brown, almost black, with small prominent warts. Peridium cream white *E. virgatosporus*
- 9. Spores without crests *E. moretii*

Varieties:

- spores 17–21 µm, with rod-like warts forming a verrucose perisporium; peridial surface with dark grey-brown granular warts, embedded in a pink-brown crust. Ascomata 10–30 mm diam, globose to irregular with ± rounded protuberances, without alliaceous or sulphuric smell. Peridium greyish white, darkening towards gleba var. *moretii*
- spores 20–24 µm, with thick rod-like warts forming a perisporium with broad and irregular meshes. Ascomata 10–30 mm diam, sometimes flattened or striate, with strong sulphuric smell. Cortex young yellowish green-grey with brown tinges, turning dark grey-brown with age. Gleba blackish green, sometimes with reddish tones var. *echinatus*
- spores 14–20 µm, with thin rod-like warts 2 µm high forming a characteristically fragmented perisporium. Ascomata 20–45 mm diam, globose, with intense smell of garlic increased while drying. Peridial surface black with prominent pyramidal warts, embedded in a dark grey-brown crust with persistent yellow spots. Peridium greyish white, slightly oxydated in blue. Gleba first reddish then dark blue var. *cantabricus*

Section *Malacodermei*

1. Mycelial coating purplish. Peridial surface purple, nearly smooth. Gleba ash-grey with bluish tones. Spores (8–)9–12(–14) µm, with thin, rod-shaped warts 1 µm high, confluent in irregular meshes *E. atropurpureus*
1. Mycelial coating white, yellowish or pinkish 2
2. Mycelial coating pink-brown to pinkish. Peridial surface grey-black, scrobiculate. Peridium cream white, slightly marbled of red tones. Gleba purplish grey-black. Spores 9–11 µm, with thick rod-like warts of various height, forming a compact irregular perisporium *E. roseolus*
2. Mycelial coating white to yellow 3
3. Mycelial layer strongly persistent, white. Peridial surface grey-black, minutely verrucose. Peridium white when cut, quickly turning bluish by oxidation. Gleba greyish blue. Spores 10–14 µm, with thick, distant, strongly incurved rod-shaped warts *E. mutabilis*
3. Mycelial coating bright yellow. Peridial surface grey-black, scrobiculate. Peridium purplish grey. Gleba brown with greyish to purplish tones. Spores 9–12 µm, with thin rod-like warts regularly arranged, 1 µm high *E. citrinus*

Acknowledgements We are grateful to the curators and herbarium managers who facilitated us the access to the collections cited here, either by arranging loans or visits in their collections: PC (Bart Buyck, Bernard Duhem, Lionel Kervran), K(M) (Bryn Dentinger, Begoña Aguirre-Hudson), LIP (Régis Courtecuisse, Christophe Lécure), PRM (Markéta Šandová), TO (Alfredo Vizzini) and MA-Fungi (Gabriel Moreno, Universidad de Alcalá). We also warmly acknowledge all mycologists who contributed to our species sampling by sending us material from their own collections: Luis Barrio de la Parte, Isabel Maria Casillas, Pascal Chautrand, Antonio De Vito, Faustino Garcia, José Luis González, Pablo Juste, Vasilios Kaounas, Kristin Killingmo, Roy Kristiansen, Jesús Linde, Marianne Meyer, Jean-Baptiste Pérez, Fernando Rodríguez, Enrique Rubio, George Setkos and Josep Maria Vidal who also contributed to the revision of *E. sulphureopallidus*, and the members of the Asociación Micológica de Algeciras Mairei, as well as Pascal Hériveau for his bibliographic assistance, Luis Alberto Parra, Karl-Henrik Larsson and Jacques Melot for nomenclatural advices, and the many colleagues and friends who supplied us with pictures, documentations and helpful discussions. Data from Norway were generated through the project 'Hypogeous macrofungi in Norway; target-oriented search for known and unknown below-ground fungi', supported by a grant from ArtsDatabanken (Norwegian Biodiversity Information Centre) to Karl-Henrik Larsson (ref.nr 67-10). Norwegian material was sequenced by Audun Schrøder-Nielsen and Virginia Mirre at Natural History Museum, University of Oslo. Data from Sweden was generated through the Swedish Taxonomy Initiative, SLU, Artdatabanken, Sweden.

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