The British species of Otidea (3): taxa present in Britain

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Abstract: An account of British species and taxa of *Otidea* is presented based on morphology and molecular data obtained from the fungarium collections, at Royal Botanic Gardens, Kew (K) and elsewhere. Based on a phylogenetic analysis using the internal transcribed spacer (ITS) sequences of the fungal nuclear rDNA, sixteen named and three unnamed taxa are recognised. Five species are being reported for the first time from Britain, which are *Otidea caeruleopruinosa*, *O. flavidobrunneola*, *O. formicarum*, *O. nannfeldtii*, and *O. tuomikoskii*. The presence in Britain is confirmed of *O. minor*, and also of *O. adorniae* and *O. parvispora*, recent segregates from *O. alutacea* which had been considered to be a species 'complex'. Reliability of using only ITS phylograms for species identification in this study has been tested by comparing them with the multiple gene analyses presented in other studies. All British *Otidea* species are of European origin. Geographical distribution and frequency of *Otidea* collections within Britain are briefly discussed.

Keywords: Ascomycota, British Funga, Pyronemataceae, phylogram, identification, taxonomy.

Introduction

A monograph of genus *Otidea* by Olariaga *et al.*. (2015) recognised 33 species worldwide, and treated 25 of them in detail. An analysis of UK collections referred to *O. alutacea* was presented by Parslow & Spooner (2015) where the variety *parvispora* was newly described. More recently, an additional species in the *O. alutacea* complex was published by Carbone *et al.*. (2019a), who also brought the variety *parvispora* up to the rank of a species. Prior to this, an account of *O. apophysata* (Cooke & W. Phillips) Sacc. and *O. platyspora* Nannf. had been given (Parslow & Spooner, 2013).

The current study aims to investigate the remaining *Otidea* species found in Britain, including some from Northern Ireland, based on specimens held in fungaria.

Discussing the phylogeny of *Otidea*, Hansen & Olariaga (2015) concluded that the ITS sequences were 'too divergent to reliably align across the breadth of *Otidea*' due to presence of gaps and tandem repeats, whereas they show low intraspecific variation (*ibid.*: 155), and that the protein-coding genes EF-1 α and RPB1 were the most effective genes for species-recognition within *Otidea*. Their multigene Bayesian phylogram based on LSU, RPB2 and EF-1 α combined (*ibid.*: 156) indicated the presence of ten clades, consistent with an all-taxa LSU phylogram presented by Olariaga *et al.*. (2015: 172–173), although a RPB1 analysis did not recognise *O. cantharella* clade (*ibid.*: 158). The ten-clade evolutionary hypothesis is accepted here, and the phylogram (Hansen & Olariaga, 2015: 156) has been used for comparison to test reliability of our species hypotheses.

As for British *Otidea* collections deposited at K, only the ITS data were available and re-sampling for extraction of other genes was not allowed. Consequently, species determinations have been carried out based on morphology and the ITS analyses only.

The species names previously applied to the fungarium collections have been reviewed. All specimens used have now been determined or re-determined and eight names have been rejected, as explained below (Results, 5.-3, 5.-4).

Material and methods

Morphological examination

610 British *Otidea* collections were examined, of which 582 are held at K, IMI, E and at other fungaria. Others were fresh material unvouchered. For comparison, 140 non-British collections were seen including those at L (21), and those received on loan from GMFN (1), H (2), HMAS (12), MICH (12) and PRM (12). Unless received fresh, each collection was rehydrated in distilled water, then slides were prepared of hand-sections, initially observed in water and measurements were made. The slides were viewed through a drawing tube at $\times 1,600$, from which pencil drawings were made. The results were

scanned and converted into JPEG images using Adobe CS6 software. In sub-micro illustrations all scale bars are of 10 μm , and in macro-images 10 mm. Melzer's reagent and 10% KOH were used for observation of hyphal encrustation in the medullary excipulum. Ultraviolet (UV) light reflection of dried and, when available, fresh specimens was seen in a dark box, through a UV filter, under a 6W UVGL-58 handheld lamp, under two wavelengths of 254 and 365 nm. The reflection was compared with the colour chart by RIDGWAY (1912) viewed under daylight, which all colour descriptions follow.

Once examined, all specimens except *O. apophysata* and *O. platyspora*, were 'grouped' based on morphological traits. Some 'groups' were immediately identifiable based on morphology. As for the rest, and for the *O. alutacea* species 'complex', naming based on morphology was hardly possible, because fresh apothecial data were often missing. To identify all 'groups' effectively, their DNA data were studied.

Phylogenetic approach

For identification purposes, the genomic DNA was extracted from 54 collections, 43 representing 11 morphological 'groups', and 11 representing variations within or taxa related to O. alutacea based on ascospore sizes and colour, using Extract-N-Amp (Sigma). The Internal Transcribed Spacer (ITS) region of the nrDNA was amplified using the primers ITS1F (GARDES & BRUNS, 1993) and ITS4 (WHITE et al.., 1990) and sequenced following Suz et al.. (2014). Obtained sequences were assembled and edited using Sequencher v. 4.2 (Gene Codes Corp.). The 42 ITS sequences newly generated in this study were preliminarily identified using BLAST searches (McGINNIS & MAD-DEN, 2004). The sequences were then aligned with 18 sequences previously held at Kew (Brock et al.., 2009, Parslow & Spooner, 2015), and with 152 ITS sequences downloaded from GenBank, referred to by OLARIAGA et al.. (op. cit.), PETERSEN (1999), HYDE et al.. (2017), Xu et al.. (2018) and Carbone et al.. (2019a). The new sequences were deposited in GenBank along with one ITS sequence which had previously been obtained but not published. The details of collections and GenBank accession numbers are given in Table 1.

Alignment was performed with MAFFT Version 7 online tool with the algorithm ('strategy') GINS-i, Scoring Matrix 1PAM/k=2 (KATOH & STANDLEY, 2013), which effectively aligned the sequences even with tandems and gaps. A phylogram was obtained under the maximum-likelihood (ML) criterion from RAXML version 8 (STAMATAKIS, 2014) with RaXMLGUI v.1.3.1 (SILVESTRO & MICHALAK, 2012), with the ITS sequence of *Monascella botryosa* as an outgroup. The GTR-GAMMA substitution model of DNA evolution was employed, and branch support was assessed using 2,000 non-parametric bootstrap replicates. Kew accession numbers, which are in the form K(M)12345, are in the phylogram expressed as K12345, to distinguish them from GenBank accession numbers with KM prefixes.

In the species accounts, specimen citation for the United Kingdom is in chronological order within a country and in a vice county. Publication dates of individual plates referred to in the text are based on the online Taxonomic Literature II (TL-2) provided by the Smithsonian Institution Libraries for the International Association for Plant Taxonomy. Publication dates of exsiccatae are based on

PFISTER (1985) and on the schedae covers preserved at K. Photographs were taken by the first author with the 'colour-balance' factor of the camera pre-set, unless otherwise stated. In some images the blue background had to be changed to a neutral colour, performed with Adobe Photoshop CS6 software, in which case a note has been made in the legend.

Table 1 – Collections included in the phylogram. Sequence given in order of GenBank accession number, species name, herbarium accession number, country of origin. Where the species name in GenBank differs from interpretation by Olariaga *et al.*. (2015), Carbone *et al.*. (2017) and Carbone *et al.*. (2019a), the interpreted name is followed by that in GenBank. The GenBank accessions generated for this study are in **bold**. Country of origin: CHN = China, DK = Denmark, ES = Spain, FI = Finland, FR = France, GE = Germany, IT = Italy, ME = Mexico, MY = Malaysia, NO= Norway, SE = Sweden. Within UK, E = England, SC = Scotland, W = Wales, NI = Northern Ireland. (CI) denotes Channel Islands.

Taxon	Туре	Country of origin	Voucher	ITS GenBank Accession no.
Monascella botryosa	TYPE	ES	CBS 233.85	NR-145208
O. adorniae	HOLOTYPE	IT	MCVE30102	NR-164497
O. adorniae		IT	MCVE30104	MK850482
O. adorniae		IT	MCVE30105	MK850483
O. adorniae		IT	MC201005 (S-F257085)	KM010069
O. adorniae		UK E	K(M)145938	KT818926
O. adorniae		UK E	K(M)81596	EU784381
O. adorniae		UK E	K(M)236326	MN627817
O. alutacea clade 3a		NO	KH.09.135 (S)	KM010064
O. alutacea clade 3a		SE	JS.08.43 (S)	KM010063
O. alutacea clade 3a		SE	KH.10.198 (S)	KM010065
O. alutacea clade 3a		SE	KH.13.50 (S)	KM010076
O. alutacea clade 3a		UK SC	K(M)201972	MN627821
O. alutacea clade 3a		UK E	K(M)127675	MN627832
O. alutacea clade 3b		DK	KS-94-192 (C)	KM010067
O. alutacea clade 3b		SE	KH.09.178 (S)	KM010066
O. alutacea clade 3b		UK E	K(M)142010	KT818924
O. alutacea clade 4		USA	Moorfun 19 (OSC)	KM010070
O. alutacea		DK	KS-94-111 (C)	KM010074
O. alutacea		ES	ARAN A3023204	KM010072
O. alutacea		FR	GC98092002	KM010073
O. alutacea		IT	MC201004 (S-F257084)	KM010075
O. alutacea		NO	KH.09.133 (S)	KM010071
O. alutacea		UK E	K(M)159266	KT818925
O. alutacea		UK E	K(M)40261	MN627827
O. alutacea		UK NI	K(M)82924	MN627828
O. alutacea		UK E	K(M)159327	MN627831
O. apophysata		GE	NV 136 (S-F257062)	KM010077
O. apophysata		UK E	K(M)87117	EU784382
O. borealis		FI	MC201009 (S-F242694)	KM010023
O. brunneoparva		FI	S-F249386	KM010024
O. brunneoparva		FI	TUR-A 198579	KM010025
O. brunneoparva		FI	TUR-A 198582	KM010027
O. brunneoparva		SE	JS.08.66	KM010028
O. brunneoparva	HOLOTYPE	SE	KH.08.107 (S)	KM010026
O. brunneoparva		SE	KH.09.82	KM010029
O. bufonia		DK	C-F-94240	KP119674
O. bufonia		DK	KH.07.37 (S)	JN942767
O. bufonia		ES	KH.09.248 (S)	JN942766
O. bufonia		FR	KH.09.249 (S)	KM010079
O. bufonia		FR	NV 2009.11.01 (S)	JN942765
O. bufonia		SE	JS.08.55 (S)	KM010078

Taxon	Туре	Country of origin	Voucher	ITS GenBank Accession no.	
O. bufonia		SE	KH.09.172 (S)	JN942764	
O. bufonia		UKE	K(M)57971	EU784383	
O. bufonia		UKE	K(M)81773	EU784384	
O. bufonia		UK E	K(M)135070	EU784386	
O. bufonia		(CI)	K(M)91376	EU784387	
O. bufonia		UK E	K(M)156215	MN627814	
O. bufonia		UKE	K(M)156216	MN627815	
O. bufonia		UK E	K(M)155699	MN627812	
O. bufonia		UK E	K(M)163424	MN627826	
O. bufonia		UK W	K(M)178805	MN627822	
O. aff. bufonia		UK E	K(M)41595	MN627811	
O. aff. bufonia		UK E	K(M)156077	MN627813	
O. caeruleopruinosa		ES	MT10082601 (SCM)	KM010030	
O. caeruleopruinosa	HOLOTYPE	FI	H6010805	NR-120285	
O. caeruleopruinosa		SE	KH.13.48 (S)	KM010081	
O. caeruleopruinosa		UK E	K(M)194835	MN627795	
O. cantharella		FR	NV 2008.09.16 (dupl. S)	KM010085	
O. cantharella		SE	JS.08.18 (S)	KM010082	
O. cantharella		SE	JS.08.47 (S)	KM010083	
O. cantharella	NEOTYPE	SE	KH.09.125 (S)	KM010084	
O. concinna		ES	KH.09.250 (S)	JN942775	
O. concinna		SE	JS.08.59 (S)	KM010031	
O. concinna	EPITYPE	SE	KH.09.183 (S)	KM010032	
O. concinna		UKE	K(M)119613	MN627803	
O. concinna		UK SC	K(M)119620	MN627805	
O. concinna		UKE	K(M)124736	MN627802	
O. concinna		UKE	K(M)237113	MN627804	
O. daliensis		ES	SEST06081702	KM010086	
O. flavidobrunneola	HOLOTYPE	FI	H6010806	NR-120286	
O. flavidobrunneola	110201112	NO	KH.09.153 (S)	KM010088	
O. flavidobrunneola		UKE	K(M)155407	MN627791	
O. flavidobrunneola		UKE	K(M)196021	MN627800	
O. formicarum		FI	H6003549	NR-120287	
O. formicarum		FI	H6003550	KM010036	
O. formicarum		NO	S-F244372 (dupl. O)	KM010034	
O. formicarum		SE	JS.08.63 (S)	KM010035	
O. formicarum		SE	KH.11.104 (S)	KM010033	
O. formicarum		UK SC	K(M)155410	MN627799	
O. hanseniae	HOLOTYPE	CHN	XF007	KU987017	
O. integra	110201112	IT	S-F108342	KP006504	
O. kaushalii		MY	TL 6236 (C)	KM010119	
O. korfii	HOLOTYPE	CHN	ZWGE1913	KU987017	
O. kunmingensis	HOLOTYPE	CHN	HKAS45492	MK850489	
O. leporina	110201112	FR	NV 2008.09.28 (dupl. S)	KM010092	
O. leporina		SE	JS.08.46 (S)	KM010092 KM010089	
O. leporina		SE SE	JS.08.92 (S)	KM010089 KM010091	
O. leporina	EPITYPE	SE	KH.09.93 (S)	KM010091	
O. leporina	LITTE	UK SC	K(M)104753	EU784388	
O. leporina		USA	OSC56784	AF072077	
O. leporina		USA	OSC56784 OSC56824	AF072077 AF072079	
O. leporina as O. myosotis	HOLOTYPE of O. myosotis	FI	H6003548	NR-120288	
	HOLOT THE OF O. THYOSOTIS				
O. minor		DK	C-F-83445	KM010038	
O. minor		DK	KH.98.94* (C) * KH.98.94 – as KH.98.84 in (KM010041	

^{*} KH.98.94 – as KH.98.84 in Olariaga et al.. (2015: 170, 219).

Taxon	Туре	Country of origin	Voucher	ITS GenBank Accession no.
O. minor		DK	TL 0754 (C)	KM010043
O. minor		FI	H6003841	KM010040
O. minor		FI	H6008618	KM010039
O. minor		IT	CL 950941-01 (dupl. S)	KM010044
O. minor		SE	KH.10.311 (S)	KM010042
O. minor		UK SC	K(M)24355	MN627806
O. minor		UK E	K(M)41748	MN627824
O. minor		UK SC	K(M)55019	MN627820
O. mirabilis		DK	KH.01.09 (C)	JN942769
O. mirabilis		FI	MC201008 (S-F257083)	KM010095
O. mirabilis	ISOTYPE	IT	S-F256929	NR-120289
O. mirabilis		SE	KH.09.188 (S)	JN942770
O. mirabilis		SE	KH.10.285 (S)	KM010094
O. mirabilis		SE	NV 108 (NV 2008.09.14) (S)	JN942768
O. nannfeldtii	HOLOTYPE	FI	H6002902	NR-120290
O. nannfeldtii		FI	S-F249387	KM010093
O. nannfeldtii		FR	NV 2008.10.01 (dupl. S)	KM010099
O. nannfeldtii		IT	CL091116-17	KM010096
O. nannfeldtii		IT	MC201011 (S-F257096)	KM010097
O. nannfeldtii		SE	JS.08.103 (S)	KM010045
O. nannfeldtii		UK E	K(M)155424	MN627801
O. nannfeldtii		USA	RH101310 (OSC)	KM010100
O. nannfeldtii as O. angusta	HOLOTYPE of O. angusta		H6010804	KF717574
O. olivaceobrunnea		CHN	HMAS23948	KU987010
O. onotica		DK	C-F-89691	JN942773
O. onotica		IT	MCVE 23277	KM010104
O. onotica		NO	KH.09.132	KM010103
O. onotica		NO	KH.09.136	JN942772
O. onotica		SE	JS.08.48 (S)	KM010102
O. onotica	EPITYPE	SE	KH.10.284 (S)	KP006505
O. onotica	22	UK SC	K(M)54800	EU784390
O. onotica		UK E	K(M)58513	EU784385
O. onotica		UK E	K(M)82864	EU784391
O. onotica		UK E	K(M)126304	EU784389
O. onotica		UK SC	K(M)155461	MN627793
O. onotica		UK E	K(M)156348	MN627794
O. onotica		UK E	K(M)157354	MN627807
O. onotica		UK E	K(M)157937	MN627792
O. onotica		UK E	K(M)237115	MN627808
O. onotica		UKW	K(M)157101	MN627825
O. onotica		UK SC	K(M)236496	MN627823
O. onotica		USA	OSC56759	AF072068
O. onotica		USA	OSC56801	AF072067
O. oregonensis		USA	Moorfun 31 (S)	KM010047
O. oregonensis	HOLOTYPE	USA	Moorfun 58 (OSC, S)	NR-155563
O. oregonensis	HOLOTTIL	USA	RH139 (S)	KM010046
O. oregonensis as O. rainierensis	+	USA	EGS2179 (MICH)	AF072093
O. oregonensis as O. rainierensis O. oregonensis as O. rainierensis	<u> </u>	USA	OSC56829	AF072093 AF072087
O. oregonensis as O. rainierensis O. oregonensis as O. rainierensis		USA	OSC56745	AF072087 AF072089
O. oregonensis as O. rainierensis O. oregonensis as O. rainierensis		USA	NSW6354 (OSC)	AF072089 AF072088
	HOLOTYPE	FI		
O. papillata	HOLOTYPE		H6003547	NR-120291
O. papillata		FI	TUR 102134	KM010105
O. parvispora		UK E	K(M)70199	EU784380

Taxon	Туре	Country of origin	Voucher	ITS GenBank Accession no.
O. parvispora		UK E	K(M)127390	MN627818
O. parvispora		UK E	K(M)135266	MN627829
O. parvispora		UK E	K(M)135268	MN627830
O. parvispora		UK E	K(M)142844	MN627819
O. parvispora		UK E	K(M)154579	MN627816
O. parvispora		UK E	K(M)237119	MN627810
O. parvispora as alutacea clade 1		DK	KH.07.46 (S)	KM010061
O. parvispora as alutacea clade 1		SE	JS.08.81 (S)	KM010062
O. parvispora as alutacea clade 1		SE	KH.09.170 (S)	KM010059
O. parvispora as alutacea clade 1		SE	KH.10.193 (S)	KM010060
O. phlebophora		DK	JV06-385 (C)	KM010049
O. phlebophora		SE	S-F108338	KM010050
O. phlebophora		UK E	K(M)143475	MN627790
O. phlebophora		UK E	K(M)33068	EU784392
O. platyspora		DK	C-F-75309	KM010108
O. platyspora		SE	HK0846 (S)	KM010107
O. platyspora		UK E	K(M)124712	EU784382
O. propinquata		FR	NV 2008.09.15 (dupl. S)	KM010111
O. propinquata		SE	JS.08.67 (S)	KM010110
O. propinquata		SE	KH.09.99 (S)	KM010109
O. pruinosa	HOLOTYPE	CHN	HKAS81819	NR-155604
O. pseudoleporina		USA	Moorfun 14 (S)	KM010113
O. pseudoleporina	HOLOTYPE	USA	RH101910 (OSC)	KM010112
O. pseudoleporina as O. concinna		USA	NSW7574 (OSC)	AF072083
O. pseudoleporina as O. concinna		USA	OSC56749	AF072082
O. pseudoleporina as O. concinna		USA	OSC56760	AF072081
O. pseudoleporina as O. concinna		USA	OSC56809	AF072080
O. purpureogrisea	HOLOTYPE	CHN	ZWGE863	KU987011
O. rainierensis	HOLOTYPE	USA	MICH14410	NR-120292
O. rainierensis as O. kauffmanii	HOLO. of O. kauffmanii	USA	MICH14409	KF717579
O. rainierensis as O. kauffmanii		USA	AH21147 (MICH)	AF072095
O. rainierensis as O. microspora	PARA. of O. microspora	USA	AH30502 (MICH)	AF072094
O. saliceticola as O. fusconigra		IT	GMFN 2293	KM010037
O. smithii		USA	ECV3345 (S)	JN942771
O. smithii		USA	OSC56753	AF072062
O. smithii		USA	OSC56799	AF072063
O. smithii		USA	OSC56811	AF072060
O. stipitata	HOLOTYPE	CHN	HKAS87865	NR-155605
O. subformicarum	110201112	ES	NV 127 (S-F256979)	KM010051
O. subformicarum		ES	S-F256980	KM010053
O. subformicarum	HOLOTYPE	ES	S-F242696	KM010054
O. subformicarum		IT	NV 95 (dupl. S-F256978)	KM010052
O. aff. subformicarum		ME	FH301035	KM010055
O. aff. subformicarum		ME	FH301036	KM010056
O. subpurpurea		CHN	HKAS54449	KU987018
O. subterranea	HOLOTYPE	USA	RH69 (FH)	NR-121353
O. subterranea		USA	RH97 (FH)	FJ404766
O. tuomikoskii	HOLOTYPE	FI	H6002901	NR-120293
O. tuomikoskii	HOLOTTIL	FR	NV 2008.09.08 (S)	JN942777
O. tuomikoskii		NO	KH.09.130 (S)	JN942777 JN942776
O. tuomikoskii		SE	JS.08.100	KM010116
O. tuomikoskii		SE	JS.08.68 (S)	KM010116 KM010114
O. tuomikoskii		SE	KH.11.77 (S)	KM010114 KM010117
O. LUUITIKUSKII		JE	N11.11.// (3)	NIVIOTOTT/

Taxon	Туре	Country of origin	Voucher	ITS GenBank Accession no.
O. tuomikoskii		SE	MK200065 (S)	KM010115
O. tuomikoskii		UKW	K(M)137478	MN627796
O. tuomikoskii		UK SC	K(M)155378	MN627797
O. tuomikoskii		UK SC	K(M)159720	MN627798
O. tuomikoskii		UK E	K(M)237118	MN627809
O. tuomikoskii		USA	OSC56756	AF072084
O. tuomikoskii		USA	OSC56761	AF072085
O. unicisa		USA	ZW-Geo65 Clark (S)	KM010118
O. sp. as bufonia		FI	MCVE 29372	MG383803
O. sp. a		SE	MK0942 (S)	KM010057
O. sp. a		SE	MK1081 (S)	KM010058
O. sp. b		SE	KH.09.79 (S)	KM010120

Results

1. Phylogenetic inference analysis

All British specimens are nested in seven well-supported clades which are comparable to those obtained in the multi-gene phylogram by HANSEN & OLARIAGA (2015: 156, obtained from the Bayesian analysis). Discrepancies were noted when the topology in our ITS phylogram (Fig. 1, split into 1a and 1b for publication) was compared to that in the said multi-gene phylogram. Contrary to the latter, in Fig. 1, *O. onotica* appears to be a sister species to all other clades except *O. papillata*, *O. alutacea* and *O. platyspora* clades, instead of being nested in one clade with *O. bufonia*.

Otidea flavidobrunneola clustered with O. bufonia and O. smithii, as in the LSU Bayesian phylogram by OLARIAGA et al.. (op. cit.: 173) and in the ITS ML phylogram by CARBONE et al.. (2019b), whereas in the said multi-gene analysis it was placed in O. concinna clade.

The position of the *O. unicisa* clade also differs, as it appears as a sister clade to the *O. tuomikoskii*, *O. leporina*, *O. formicarum* and *O. concinna* clades combined, whereas in the multi-gene phylogram it appears as a sister clade to the *O. concinna*- and *O. bufonia-onotica* clades.

The topology within the *O. alutacea* clade in Fig. 1 differs only slightly from the ITS-LSU consensus phylogram by CARBONE *et al.*. (2019a: 119), in that *O. parvispora* is shown as a well-supported sister species to the rest of the clade, whereas in the latter, *O. adorniae* is in a position separate from the rest of the clade.

2. Species identifications based on ITS sequences

In total, 16 named species and three unnamed taxa are here recognised. Of the three unnamed taxa, two belong to the *O. alutacea* clade (see 4.-4b, 4.-4c), whilst the third is phylogenetically related to *O. bufonia* (see 4.-6a), and needs further investigation.

Prior to this study, the presence of three species in Britain had been confirmed with morphology and molecular data: *Otidea apophysata* (Cooke & W. Phillips) Sacc., *O. platyspora* Nannf. (Parslow & Spooner, 2013), and *O. alutacea* (Pers.) Massee *sensu stricto* (*sensu* Olariaga *et al..*, see Parslow & Spooner, 2015). The latter authors recognised three taxa within *O. alutacea s. lat.* in Britain (*loc. cit.*), which refer to clades 1 & 3b in Olariaga *et al.*. (*op. cit.*) and a new clade, and described clade 1 as *O. alutacea* var. *parvispora*. More recently, Carbone *et al..* (2019a) raised this variety to the rank of species, *O. parvispora* (Parslow & Spooner) M. Carbone *et al..*, based on an ITS-LSU consensus phylogram, and described a new species, *O. adorniae* Agnello *et al..* based on the 'new clade' (Parslow & Spooner, 2015, later numbered as clade 5 by Xu *et al..*, 2018). Two new species, *O. parvispora* and *O. adorniae*, are hereby accepted as British.

Yet another taxon of *O. alutacea* in Britain, clade 3a of OLARIAGA *et al.*. (*op. cit.*), has now been identified. Our ITS phylogram indicates

that the clades 3a and 3b cluster closely with that of *O. alutacea s. str. sensu* OLARIAGA *et al.*. (*op. cit.*), as consistent with the ITS-LSU phylogram by CARBONE *et al.*. (2019a). Apothecial morphology of species in these two clades overlaps, as explained below, and assignation of *O. alutacea s. str.* to a particular clade remains questionable (PARSLOW & SPOONER, 2015). Therefore, the remaining clades are not named in this study.

Five species previously reported as British (RAMSBOTTOM & BALFOUR-BROWNE, 1951; CANNON et al.., 1985) have here been accepted, viz.: Otidea onotica (Pers.) Fuckel; O. bufonia (Pers.) Boud.; O. leporina (Batsch) Fuckel; O. concinna (Pers.) Sacc. and O. phlebophora (Berk. & Broome) Sacc.

Five species are reported for the first time as British: *Otidea caeruleopruinosa* Harmaja; *O. flavidobrunneola* Harmaja; *O. formicarum* Harmaja; *O. nannfeldtii* Harmaja and *O. tuomikoskii* Harmaja.

The presence in Britain of *Otidea minor* (Boud.) Olariaga & K. Hansen had previously been suggested by a 1977 collection (K(M)41748, as *O. cantharella* var. *minor* Boud.). In this study, K(M)41748 was 'grouped' with similar specimens previously named as *O. phlebophora*, and based on the ITS sequence and the phylogenetic inference analysis, has been confirmed as *O. minor*. Two other collections formerly referred to *O. phlebophora* have been redetermined as such.

Two specimens, K(M)41595 and K(M)156077, have been found to belong to an unnamed taxon related to *O. bufonia* and *O. subpurpurea* W.Y. Zhuang, for which see 4.-6a.

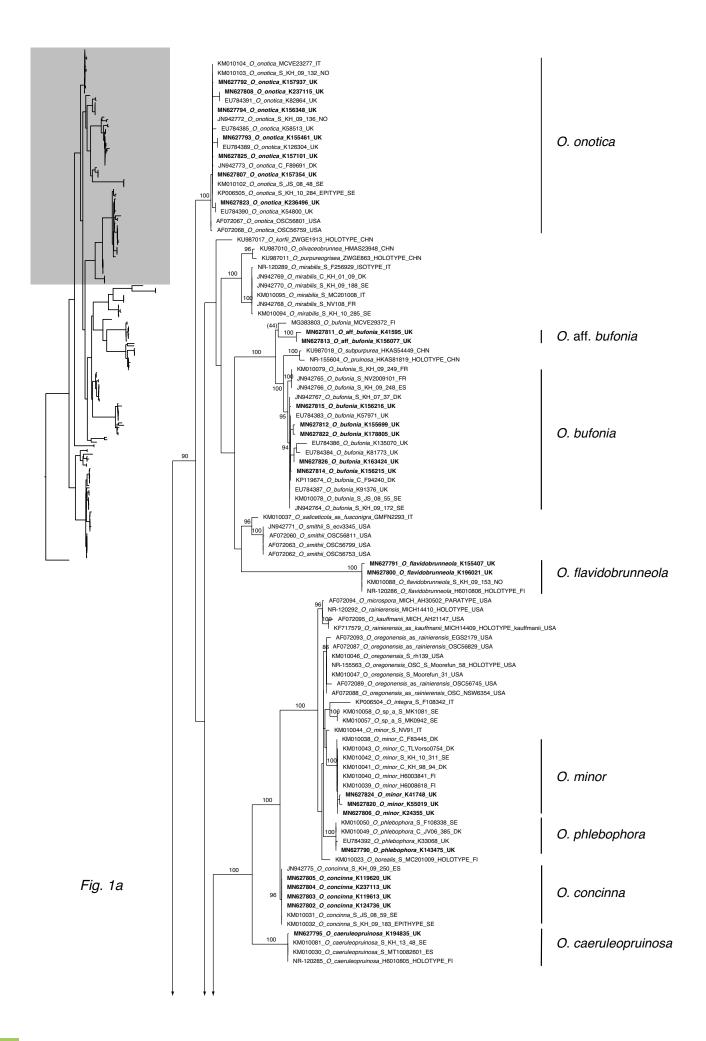
Whether species in the *O. cantharella* clade are truly absent from Britain, or are yet to be discovered (see 4.-17), remains to be resolved.

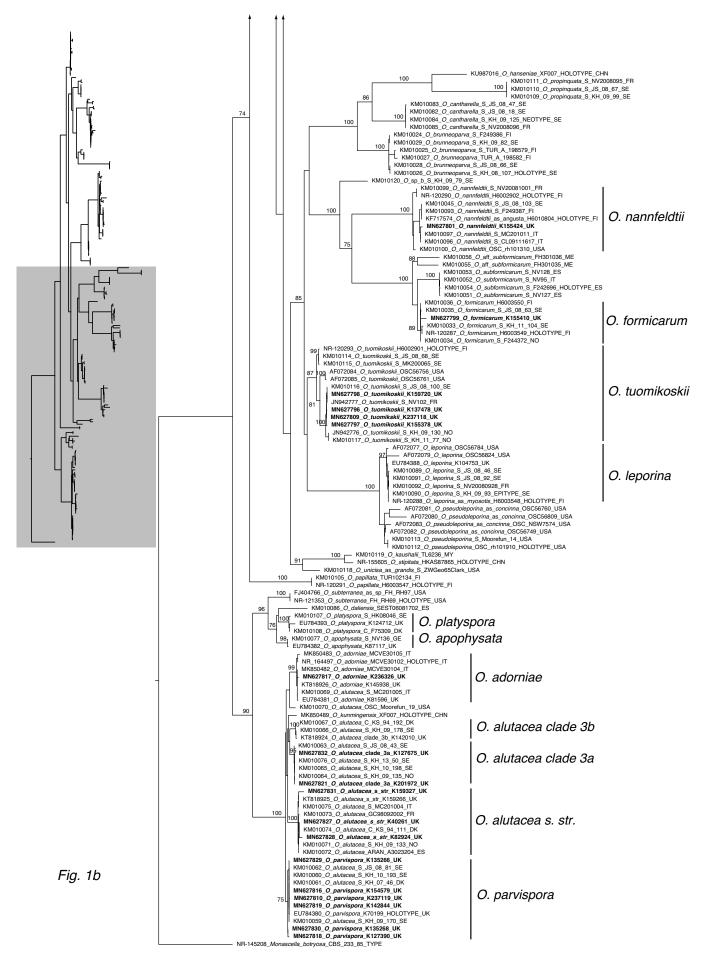
3. Distribution and frequencies of collections of *Otidea* within Britain

The 573 British *Otidea* collections held at K, and their countries (including the Channel Islands) of origin are summarised in Table 2. Material borrowed from other fungaria, as well as some fresh collections seen but not deposited at K, and records without a voucher, are excluded.

A simple chi-squared test performed on the re-arranged data, in which the numbers of collections from Northern Ireland and that from Channel Islands are combined, rejected a null hypothesis that locations of origins of *Otidea* at K are randomly distributed over Britain, with probability 0.001. As expected, the *Otidea* collections

Fig. 1a, 1b (next pages) – Best-scoring ITS phylogram obtained from 212 Otidea ITS under Maximum likelihood criterion. The dataset was aligned with MAFFT online tool and phylogram created using RAxML v8 analysis with 2,000 bootstrap replicates. Nodes are annotated where supported ML bootstrap value >70%.





0.1

held at K have an English bias most probably because there have historically been more mycologists in England. The bias is less apparent in that of rarer species found under a specific habitat, for example, *O. tuomikoskii* under *Picea* spp.

The most frequently collected species of *Otidea* in Britain are *O. onotica* and *O. bufonia*. Although CARBONE *et al.*. (2019a) suggested that there are two lineages in *O. bufonia* in Europe, we have found British sequences in only one of them, 'lineage 2'.

O. leporina has proven to be uncommon. Prior to our study there

were 87 British collections held under that name, mostly from midto late-19 century. The oldest, K(M)156052, originated from Herb. J. Sowerby (ex British Museum) and is considered to be from the period between 1780 and 1820. Most of them have been re-identified, including the Sowerby specimen (as *O. bufonia*), only four now retaining the name. A further collection of this species was found in the *O. alutacea* folder at K.

For redisposition of the older collections at K, see the species accounts below.

Table 2 – Countries of origin of *Otidea* specimens from Britain held at K and Herb IMI. A collection marked 'possibly from England' and another 'possibly from Scotland' are included in the relevant region respectively. Specimens from the Hebrides and the Clyde Isles are included in Scotland. No *Otidea* collections preserved originated from the Isle of Man.

Country / area	England	Wales	Scotland	Northern Ireland	Channel Islands	Total	
Area km²	130395	20735	80077	14130	198	245535	
Area proportion	0.531	0.084	0.326	0.058	0.001	1	
Species / taxa	Number England	Number Wales	Number Scotland	Number Northern Ireland	Number Channel Islands	Sub- total	%
O. alutacea s. str. (determined)	3			1		4	0.70
O. alutacea clade 3b (determined)	1					1	0.17
O. alutacea clade 3a (determined)	1		1			2	0.35
O. alutacea large-spored taxa*	79	8	3			90	15.71
O. alutacea small-spored taxa**	52		3	2		57	9.95
O. adorniae (determined)	3					3	0.52
O. parvispora (determined)	5					5	0.87
O. apophysata and related taxon	19					19	3.32
O. platyspora	12					12	2.09
O. bufonia	122	11	8	2	1	144	25.13
A related taxon	2					2	0.35
O. onotica	134	11	20			165	28.80
O. leporina	3		2			5	0.87
O. caeruleopruinosa	2					2	0.35
O. concinna	11	2	2			15	2.62
O. flavidobrunneola	2					2	0.35
O. minor	1		2			3	0.52
O. phlebophora	11		4			15	2.62
O. formicarum	1		1			2	0.35
O. nannfeldtii	1					1	0.17
O. tuomikoskii	1	2	2			5	0.87
O. spp	13	3	2	1		19	3.32
Total	479	37	50	6	1	573	100.00

^{*} Expected to include O. alutacea s. str. and clade 3b. ** Expected to include O. adorniae, O. parvispora and O. alutacea clade 3a.

4. Species accounts

The species accounts, below, have been arranged for each clade recognised in the multi-gene analysis by Hansen & Olariaga (op. cit.). Thus, O. flavidobrunneola is placed in the O. concinna clade. Only specimens confirmed by molecular data are given unless stated otherwise, accompanied with notes. For detailed descriptions and specimens of O. apophysata and O. platyspora, see Parslow & Spooner

(2013). For *O. alutacea s. str.* and *O. parvispora* (as *O. alutacea* var. *parvispora*), see Parslow & Spooner (2015). Previous usage of names by British authors follow Ramsbottom & Balfour-Browne (1951) and Cannon *et al.*. (1985) unless specified otherwise. In the descriptions, the 'crystals' on the ectal excipular cells equate to 'resinous exudates' in Olariaga *et al.*. (*op. cit.*); their main component is calcium oxalate, in some species pigmented with unknown components (Parslow &

SPOONER, 2013). Where necessary, the descriptions have been supplemented with colour information of fresh apothecia from OLARIAGA et al.. (op. cit.), HARMAJA (2009), and CARBONE et al.. (2019a). General characters common to all European Otidea species (e.g. ascospores are ellipsoid, or its variant, with two guttules and smooth epispore, and that the asci are inamyloid and arise from a crozier, etc.) are not stated for each species.

Otidea platyspora clade

4.-1 Otidea apophysata (Cooke & W. Phillips) Sacc., Syll. fung., 8: 96 (1889).

Basionym: *Peziza* (*Cochleatae*) *apophysata* Cooke & W. Phillips, *Grevillea*, 5: 60 (1876).

British types: ENGLAND, Shropshire, Shrewsbury, Copthorne, Oct. 1876, Phillips, holotype, K(M)30410; isotype, K(M)167215 (a half of the holotype specimen).

Specimen: ENGLAND, Surrey, Kew, Royal Botanic Gardens, Kew, 17 Aug. 2001, Henrici, K(M)87117.

Notes: Known from fourteen localities in England, mostly from damp habitats. See Parslow & Spooner (2013) for detailed descriptions and illustrations.

Summarised description: Apothecia dark brown, drab coloured cup-shaped, unequal, split on one side, solitary or in small clusters; ectal excipulum with pale yellow pigmented walls, not or only rarely and slightly encrusted with pale brown or yellowish crystals, ascospores broad-fusoid, $(20.5-)21.5-26.5 \times (10.0-)10.5-12.5 \mu m$, 1.94 < Q < 2.24.

Distribution outside Britain: France, Germany, Belgium and Spain (Parslow & Spooner, 2013, Olariaga *et al..*, 2015).

4.-2 *Otidea platyspora* Nannf., *Ann. bot. fenn.*, 3: 317 (1966).

Specimen: ENGLAND, Northamptonshire, Bedford Purlieus, 27 Jul. 2004, Wells, K(M)124712.

Exsiccatae: SWEDEN, Uppland, Aug. 1895, Starbäck, K(M)158886, Rehm, *Ascomyceten* 1153; Uppland, Danderyd, Djursholm, Oct. 1951, Zander, K(M)158871, Lundell *et al..*, *Fungi Exsiccati Suecici* 3284.

Notes: Known from ten localities in England, mostly from dry paths, parks, or cemeteries. In addition to the ten specimens reported previously, two others have been located amongst old accessions: Somerset, Yeovil, Clifton Wood, 8 Aug. 2010, Legon, K(M)176380. South Hampshire, Beaulieu, Culverley, 27 Oct. 2002, Reid & Ainsworth, K(M)199169. See Parslow & Spooner (2013) for detailed descriptions and illustrations.

Summarised description: Apothecia dark brown or dirty grey, drying lighter to wood-brown colour, clustered and coalescent, split on one side, ectal excipulum locally and only slightly encrusted with brown crystals, or not; ascospores broad ellipsoid, rounded at ends, $(17.0-)18.0-22.0(-24.0)\times10.5-13.0~\mu m$, 1.61<Q<2.00.

Distribution outside Britain: Scandinavian countries, France, Germany, the Netherlands, and Azerbaijan (OLARIAGA *et al..*, 2015).

Otidea alutacea clade

4.-3 Otidea adorniae Agnello, M. Carbone & P. Alvarado, *Ascomycete.org*, 11 (4): 121 (2019).

Confirmed here as a British species.

Specimens: ENGLAND, Leicestershire, Leicester, 28 Nov. 2006, Rixon, K(M)145938; Oxfordshire, Oxford, under *Quercus* sp., 12 Oct. 2000, Webb, K(M)81596; Surrey, Long Ditton, Church Road, under *Fagus* sylvatica f. purpurea, 11 Aug. 2017, E. Brown, K(M)236326.

Notes: Formerly reported as an un-numbered clade related to *O. alutacea* (Parslow & Spooner, 2015), recently described as a new species. The ascospore ranges, Q, and variations in hymenial colour of *O. adorniae* (Carbone *et al..*, 2019a: 121) overlap with those of *O. parvispora* (Parslow & Spooner, 2015: 298, and see 4.-5); thus these two species could not safely be distinguished based on morphological diagnoses only. Determination of any given specimen should be confirmed with DNA.

Summarised description: Apothecia in small clusters, ear-shaped when young (Carbone *et al..*, 2019a). British collections cupshaped, truncate, colour Fawn (XL13""), drying Warm Buff (XV17'd). Hymenium in original description ochraceous brown to brown' (Carbone *et al..*, *loc. cit.*, holotype MCVE30102, Italy), however, in British collections hymenium Warm-Buff (XV17'd) to Tawny (XV13'i), drying Warm-Buff (XV17'd), not brown. Ectal excipular cells not encrusted with Ca-ox crystals. Paraphyses with hyaline or pale yellow granulate inclusion. Ascospores in original description (10.5–) 11–12 (–12.5) × 6–6.5 (–7) μ m, 1.7<Q<1.95, with which K(M)236326 is in accordance, but not K(M)81596, in which spores are 12.5–14.5 × 6.2–7.5 μ m, 1.93<Q<2.02. For aberrant K(M)145938 see Parslow & Spooner (2015: 301).

Distribution outside Britain: Italy (CARBONE et al.., op. cit.).

4.-4 Otidea alutacea (Pers.) Massee, *Brit. Fung.-Fl.*, 4: 446 (1895). Basionym: *Peziza alutacea* Pers., *Observ. mycol.*, 2: 78 (1799).

4.-4a O. alutacea sensu stricto (sensu Olariaga et al..)

Specimens: ENGLAND, Berkshire, Ramsbury Wood, 27 Sep. 1994, Storey, K(M)40261; South Essex, Epping Forest, under Fagus sylvatica, 25 Aug. 2008, Kibby, K(M)159266; South Hampshire, New Forest, under *Quercus robur*, Aug. 2008, Hughes, K(M)159327. Northern Ireland, Fermanagh, Castle Archdale Country Park, near *Fagus sylvatica*, 14 Oct. 2000, Jeffries, K(M)82924.

Summarised description: Apothecia in small clusters, cupshaped but margin undulate and variable, split, colour Fawn (XL13""), drying Pale Ochraceous-Buff (XV15'f), partly Warm Buff (XV17'd), hymenium Russet (XV13'k) except K(M)82924 in which it is Warm Buff (XV17'd). Ectal excipular cells not or hardly encrusted with Ca-ox crystals. K(M)159266 has ascospores 15.5–17.0 (–18.0) × 7.0–8.0 µm, 1.99<Q<2.34, av. 2.16 (n=38), and is macro- and microscopically indistinguishable from K(M)142010, clade 3b (PARSLOW & SPOONER, 2015). In other collections spores are 15.0–16.5 µm, 1.99<Q<2.42. The latter measurement is in accordance with that of KH09.133 in Hansen & Olariaga (*op. cit.*), Fig. 6, p. 160, as *O. alutacea* (1). Ascospore sizes alone are insufficient to distinguish the clade in which any given specimen is to be placed. K(M)40261 is with slight hyaline encrustation on part of ectal excipular cells.

Notes: See Parslow & Spooner (2015) for detailed descriptions and illustrations.

Distribution outside Britain: Known from Scandinavian countries, France, Italy, and China (Olariaga *et al..*, *op. cit.*; Xu *et al..*, 2018).

4.-4b O. alutacea clade 3a

Specimens: England, West Lancashire, Carnforth, 18 Aug. 1992, Leedal, K(M)127675. Scotland, Wester-Ross, Ullapool, under *Fagus sylvatica*, 27 Aug. 2014, Cannon, K(M)201972.

Summarised description: In both specimens apothecia resemble those of *O. alutacea s. str.*, ectal excipular cells not encrusted with Ca-ox crystals, ascospores 13.4–15.5 \times 6.0–6.4 μ m, 2.22<Q<2.42, hymenium Ochraceous-Tawny (XV15'i) when dry.

Notes: Morphology of the specimens overlaps with that of *O. alutacea s. str.*, and that of *O. parvispora*, below. British sequences clustered tightly with those of clade 3a downloaded from GenBank (ident. >99%), but when BLAST-analysed are also close to a Danish collection KS 94 192 in clade 3b and two Chinese collections referred to by Xu *et al.*. (2018, ident. >97%).

Distribution outside Britain: Scandinavian countries (OLARIAGA *et al.., op. cit.*), Italy (CARBONE *et al..,* 2019a), Germany (LM4111, Gen-Bank data).

4.-4c O. alutacea clade 3b

Specimen: ENGLAND, West Gloucestershire, Westonbirt Arboretum, under *Fagus sylvatica*, 15 Oct. 2006, Alder, K(M)142010.

Summarised description: Morphologically indistinguishable from K(M)159266, *O. alutacea s. str.* except in having slightly denser subhymenial pigmentation, thus drying Dresden Brown (XV17'k).

Ectal excipular cells not encrusted with Ca-ox crystals, ascospores 15.5–17.0 (–18.0) \times 7.0–8.0 $\mu m,~2.00 < Q < 2.21,~av.~2.14 (n=36) (Parslow & Spooner, 2015).$

Notes: Morphological similarity with *O. alutacea s. str.* raises doubt in the interpretation of the epithet 'alutacea', which remains to be resolved. The sequence of K(M)142010 clusters tightly with others of clade 3b from GenBank (ident. >99%) but when BLAST-analysed is closely related to those belonging to other clades, for example a Chinese collection referred to by Xu *et al.*. (2018, ident. 97%) and another by Carbone *et al.*. (2019, >98%).

Distribution outside Britain: Scandinavian countries (OLARIAGA et al.., op. cit.).

4.-5 *Otidea parvispora* (Parslow & Spooner) M. Carbone, Agnello, Kautmanová, Z.W. Ge & P. Alvarado, *Ascomycete.org*, 11 (4): 121 (2019).

Confirmed here as a British species.

Basionym: *O. alutacea* var. *parvispora* Parslow & Spooner, *Ascomycete.org*, 7(6): 297 (2015).

British type: ENGLAND, Surrey, Kew, under *Quercus ilex*, 19 Oct. 2000, Legon, K(M)70199, holotype. Index Fungorum Identifier 551565.

Specimens: England, East Suffolk, Flatford Mill, 12 Oct. 2002, Kibby, K(M)237119; Huntingdonshire, Buckden, Little Paxton Gravel Pits, near *Quercus cerris*, 30 Oct. 2004, Parslow, K(M)127390; Huntingdon, Hinchingbrooke Country Park, 9 Oct. 2005, Wells, K(M)135266; Buckden, Little Paxton, 17 Oct. 2005, Wells, K(M)135268; South Wiltshire, Shaftesbury, Swallowcliffe churchyard, under *Cedrus* sp., 7 Sep. 1971, Hindley, K(M)154579; West Kent, Southborough Cemetery, under *Cedrus* sp., 7 Nov. 2006, Weightman, K(M)142844.

Notes: Previously reported and described as a variety within *O. alutacea*, recently raised to the rank of species. Ascospore sizes and apothecial colour overlap with *O. adorniae* (see 4.-3). See also Parslow & Spooner (2015) for detailed descriptions and illustrations.

Summarised description: Apothecia in small clusters, shallow cup-shaped, split, colour Fawn (XL13""), drying Warm Buff (XV17'd), hymenium mostly Light Ochraceous-Buff (XV15'd), drying Warm-Buff (XV17'd), however in K(M)135266 and K(M)135268 hymenium darker, Dresden Brown (XV17'k). Ectal excipular cells not encrusted with Ca-ox crystals. Paraphyses with hyaline or pale yellow granulate inclusion. Ascospores in holotype, (11.0–) 11.5–13.0 \times 5.0–6.5 µm, 1.73 < Q < 2.28, av. 2.04 (n=41), the rest within 11.5–14.0 \times 5.0–6.5 (–7) µm, except K(M)154579, 12.5–14.5 \times 6.0–7.0 µm, extending Q range max. to 2.30.

Distribution outside Britain: Scandinavian countries (OLARIAGA *et al.., op. cit.*), France (VAN VOOREN, 2017), Spain, Greece (CARBONE *et al..,* 2019).

Otidea bufonia - onotica clade

4.-6 Otidea bufonia (Pers.) Boud., Hist. class. discom. Eur.: 52 (1907).

Basionym: Peziza bufonia Pers., Mycol. eur., 1: 225 (1822).

Names used by British authors:

Otidea grandis (Pers.) Boud., Bull. Soc. mycol. Fr., 9(1): 10 (1893). Peziza umbrina Pers., Observ. mycol., 2: 77 (1799).

Scodellina umbrina (Pers.) Gray, Nat. Arr. Brit. Pl., 1: 668 (1821).

Otidea umbrina (Pers.) Bres., Fung. Trident., 2: 68, pl. 180 (1892).

History of British usage of the name: In the 19th century, British authors misapplied the name *Peziza bufonia* to a fungus with large spores, $20-24 \times 10-12$ µm (Cooke, 1877: 169, pl. 292; Phillips, 1887: 75; Massee, 1895: 430). Bresadola (1898: 77) considered Cooke's illustration pl. 292 to be *Peziza granulosa* Schumach. The species which we now know as *O. bufonia* had in Britain most frequently been called *Peziza grandis* or *O. grandis* (as in Cooke, 1879, pl. 376; Phillips, 1887; Massee, 1895) due to Rehm's application of this name to *O. bufonia* in *Ascomyceten* 651 (a lithograph-offset label, Rehm, 1882). The name *O. grandis* was not validated then due to insufficiency of the

label, nor in his later publication (REHM, 1883) in which no. 651 was printed as '? O. grandis'. Validation was made by BOUDIER (1893) who, however, illustrated O. grandis (BOUDIER, 1908b, pl. 328) as distinct from O. bufonia (BOUDIER, 1908a, pl. 330) based on its hymenium colour. This distinction was reflected in ELLIS & ELLIS (1988: 85). OLARIAGA et al.. (2015) examined Boudier's O. grandis specimen which proved to be O. bufonia. For synonymy of O. umbrina with O. bufonia, see Parslow & Spooner (2013).

Selected specimens: ENGLAND, Dorset, The Isle of Purbeck, Studland, under *Salix* sp., 15 Sep. 2008, Robinson, K(M)163424; Middlesex, Buckingham Palace garden, 13 Jul. 1998, Henrici, K(M)57971; South Lancashire, Formby, Freshfield, under *Salix fragilis* and *Alnus glutinosa*, 8 Sep. 1963, Palmer & Kotlaba, K(M)155699; Surrey, Brentmoor Heath, near *Quercus* sp. and *Fagus sylvatica*, 18 Oct. 2005, Tantram, K(M)135070; West Cornwall, Mawnan, near *Quercus ilex*, 9 Nov. 2000, Roberts, K(M)81773. West Kent, Oldbury, 16 Oct. 1980, Pitt, K(M)156215; West Sussex, The Mens Nature Reserve, 8 Sep. 1979, Reid, K(M)156216. WALES, Anglesey, Newborough Warren, under *Pinus* sp., 24 Sep. 2001, Leonard, K(M)178805. CHANNEL ISLANDS, Jersey, Saint Brelade, near *Quercus ilex*, 5 Nov. 2001, Armstrong, K(M)91376.

Selected specimens based on morphology only: ENGLAND, Surrey, Frensham, 28 Aug. 1950K(M)156287. Scotland, West Perthshire, Crossgates, 9 Sep. 1980, R. Phillips, K(M)156334.

Exsiccatae: GERMANY, Brandenburg, Berlin, Zehlendorf, under *Quercus* sp., Aug. 1882, Sydow, K(M)160827, Rehm, *Ascomyceten* 651, sub *Otidea grandis*; Berlin, Zehlendorf, Sep. 1881, Sydow, K(M)262976, Rabenhorst-Winter, *Fungi europaei* 2650; Nordrhein-Westfalen, Oestrich, circa 1864, K(M)158620, Fuckel, *Fungi Rhenani* 1230, sub *Peziza cochleata* Bull.

Selected British illustrations of *O. bufonia* **based on morphology:** DENNIS (1968, pl. 5 C; 1978, 1981, pl. 8 C, all painted from K(M)156287); R. PHILLIPS (1981, *Mushrooms and other fungi of Great Britain and Europe*, p. 270, photograph, of K(M)156334).

Notes: The lectotypification of *Otidea bufonia* by Olariaga *et al.*. (*op. cit.*) with Persoon's L0116690 / 911.81.97 determined the identity of this species. Eight British collections previously named *O. grandis* (and *O. umbrina*) at K have been re-named as *O. bufonia* (7), and as *O. alutacea* (1).

This species is widespread in Britain and most frequently is collected in dry, thermophilous woodland in England. Known to be ectomycorrhizal from GenBank data, 24 out of 144 British collections are associated with *Quercus* sp., eight with *Fagus sylvatica*, five with *Salix* sp., four with *Pinus sylvestris*. CARBONE et al.. (2019a) indicated the presence of two phylogenetic lineages of *O. bufonia* in Europe, but all British sequences belong to only one of them (lineage 2).

Species description: Apothecia gregarious, or clustered in two or rarely three. Excipular colour and appearance brown to purplish brown when fresh, Olive-Brown (XL17"'k) or Buffy Brown (17"i) when dry, scurfy with small pustules. Frequently with buff or pale basal tomentum. Hymenial colour ochre-brown or brown, opaque when fresh, Olive-Brown (XL17"'k), Bister (XXIX15"m) or Natal Brown (XL13"'k) when dry. Ectal excipulum of textura angularis, cells globose when rehydrated, with outgrowths in chains, densely encrusted with dark yellow-brown pigmented Ca-ox crystals. Subhymenium pigmented pale yellow or pale yellowish brown. Medullary excipulum in contrast to subhymenium, hyaline or very pale yellow at most. Brown encrustation on the hyphae present, some striate in appearance along the circumference ('fingerprint hyphae' fide Korf & Zhuang, 1991), abundant in most British specimens, rarely almost absent, or only localised near the margin. Paraphyses not or only slightly swollen at apices, 3 µm wide at middle, filled with hyaline or pale yellow granulate substance when fresh, monotonous pale yellow when dry, 3–3.5 μm wide at middle, curved above and slightly hooked, slightly swollen to $4.0-4.5~\mu m$ at apices, with hyaline or pale yellow granulate inclusion. Ascospores characteristically ellipso-fusoid, narrowed at both ends, (13-) 15.0-16.0 (–17) \times 6.0–7.0 μm. Asci 150–180 \times 10–11 μm. UV reactions

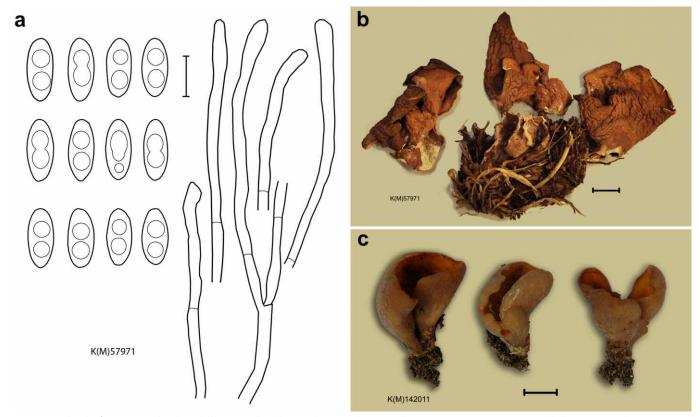


Fig. 2 – Otidea bufonia; a: England, Middlesex, Buckingham Palace garden, 13 Jul. 1998, Henrici, K(M)57971. Scale bar = 10 μm; b: K(M)57971. Scale bar = 10 mm; c: England, Surrey, Brentmoor Heath, 22 Oct. 2006, Alder, K(M)142011. Scale bar = 10 mm.

when dry: outer surface smoky-black or Clove Brown (XL17"m) under 254 nm, Clove Brown (XL17"m) or Deep Olive (21"k) under 365 nm, hymenium Vinaceous-Buff (XL 17"d), Tilleul-Buff (17"f), or Pale Smoke Gray (XLVI 21"f) under 254 nm, Pale Olive-Buff (XL21"f) or Pale Smoke Gray (XLVI 21"f) under 365 nm. Encrustation of basal mycelium: small brown crystals at places, no colour reaction to KOH.

Distribution outside Britain: Widespread in Europe, suggested present in North America and China (OLARIAGA *et al..*, *op. cit.*).

4.-6a An unnamed taxon related to O. bufonia

As stated in 2, K(M)41595 and K(M)156077 belong to an unnamed taxon related to *O. bufonia* and *O. subpurpurea* W.Y. Zhuang. Morphologically, they resemble *O. bufonia*, only differing in colour and distribution of dark encrustation on the medullary excipular hyphae. These two, along with another, K(M)41596, were collected on the same day from a single locality in North Yorkshire, only 2 metres apart from each other, but showed differing apothecial colour, and were examined by W.D. Graddon (Graddon's notes, preserved at the archive of Royal Botanic Gardens, Kew, hereafter RBG, Kew). They certainly belong to the same taxon, and quite probably to the same hyphal mass underground. The status of this taxon needs to be investigated.

In Fig. 1, the ITS sequences from these collections cluster with a Finnish specimen MCVE29372, but only with weak support, and thus are probably not conspecific with the latter.

4.-7 Otidea onotica (Pers.) Fuckel, *Jahrb. Nassauischen Vereins Naturk.*, 23-24: 329 (1870).

Basionym: Peziza onotica Pers., Syn. meth. fung.: 637 (1801).

Names used by British authors:

Peziza leporina, sensu Sowerby, Col. Fig. Engl. Fung., 1, pl. 79 (1797). Scodellina onotica (Pers.) Gray, Nat. Arr. Brit. Pl., 1: 668 (1821).

History of British usage of the name: COOKE (1878, pl. 210) and PHILLIPS (1887: 52) used Persoon's original *Peziza* combination. The latter referred *Peziza* onotica to the subgenus *Otidea* but his illustration (pl. 3, fig. 13) shows spores very roughly ornamented and with

one guttule, thus unlikely to be of an *Otidea*. Fuckel (1870: 329) made an *Otidea* combination which was later adopted by Massee (1895: 447) and by subsequent British authors. Twelve 19th-century *O. onotica* specimens at K were previously misidentified as *O. leporina*.

Selected specimens: ENGLAND, Berkshire, Sunninghill, Aug. 1974, Green, K(M)157354; Derbyshire, Deepdale, 26 Oct. 2004, Kelly, K(M)126304; Herefordshire, Ludlow, under *Pseudotsuga menziesii*, 1 Oct. 2017, Weightman, K(M)237115; Leicestershire, Charnwood, 19 Sep. 1965, Fieldhouse, K(M)157937; North Lincolnshire, Woodhall Spa, under *Pinus* sp. etc., 13 Sep. 1986, Holden, K(M)156348; North Northumberland, Rothbury, under *Pinus* sp., 27 Aug. 1998, Ellis, K(M)58513; Surrey, Aldershot, under *Fagus sylvatica*, 21 Oct. 2000, Legon, K(M)82864; South Wiltshire, Clanger Wood, under *Fagus sylvatica*, 15 Nov. 1998, Gange, K(M)236496. Scotland, Mid Perthshire, Aberfeldy, under *Fagus sylvatica*, 5 Sep. 1997, Spooner, K(M)54800; North Ebudes, Isle of Rhum, under *Picea* sp. 30 Sep. 1961, Dennis, K(M)155461. WALES, Caernarvonshire, Snowdonia National Park, Gwydyr Forest, 6 Oct. 1979, Brown, K(M)157101.

British exsiccatum: Scotland, Mid Perthshire, Perth, 1870, K(M)155486, Cooke, *Fungi Britannici Exsiccati* 365.

Selected British illustrations: Sowerby (1797, pl. 79), as *O. leporina*; Cooke (1876, pl. 53, fig. 210); Dennis [1968, pl. 5 A, painted from K(M)41592].

Note: Having rejected Carbone's typification (2009), Olariaga *et al.*. (2015) lectotypified this species with Sowerby's illustration pl. 79 as *Peziza leporina* (1797), and designated a recent Swedish collection, KH.10.284, as epitype. All British sequences cluster in the same clade with the epitype, though some indicating the presence of intraspecific lineages which, however, do not present morphological distinctions. Currently accepted as one species, *O. onotica* is one of the *Otidea* species most frequently collected in Britain. Harmaja (2009) considered this species a calciphile in Finland but it is widespread in Britain and has been collected from various soil types. Confirmed to be ectomycorrhizal from GenBank data, *Fagaceae* woodland is particularly favoured, but *Betulaceae*, *Pinus sylvestris*, *Abies* spp., *Picea* spp., and *Pseudotsuga menziesii* are all known hosts.

This species has large, ear-shaped apothecia, creamy salmon when fresh, often with pink spots on hymenium but may be misidentified when immature or when lacking pink spots. When dry, the receptacles gain dark, warm brown colours. When under UV lights, the dark receptacle and the pale hymenium contrast strongly.

Species description: Apothecia ear-shaped, clustered, rarely truncate, up to 100 mm tall, 70 mm wide, expanding with age, some becoming subsessile. Outer surface Pale Ochraceous-Salmon (XV13'f) when fresh, warty or scurfy, drying Ochraceous-Tawny (XV15'i), Buckthorn Brown (XV17'i), or rarely Dresden Brown

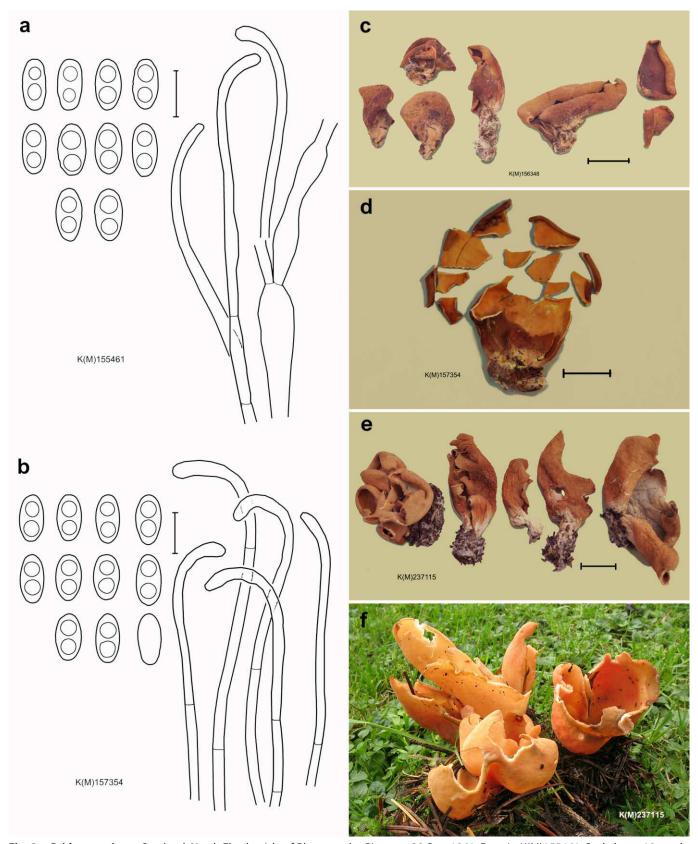


Fig. 3 – *Otidea onotica*; a: Scotland, North Ebudes, Isle of Rhum, under *Picea* sp., 30 Sep. 1961, Dennis, K(M)155461. Scale bar = $10 \mu m$; b: England, Berkshire, Sunninghill, Aug. 1974, Green, K(M)157354. Scale bar = $10 \mu m$; c: England, North Lincolnshire, Woodhall Spa, under *Pinus* sp. etc., 13 Sep. 1986, Holden, K(M)156348, hymenium drying Mahogany. Scale bar = $10 \mu m$; d: K(M)157354, showing hymenium drying Ochraceous Tawny. Scale bar = $10 \mu m$; e: K(M)237115, England, Herefordshire, Ludlow, under *Pseudotsuga menziesii*, 1 Oct. 2017, Weightman, hymenium drying Ochraceous Salmon. Scale bar = $10 \mu m$; f: K(M)237115, fresh apothecia.

(XV17'k), hymenium when fresh most often with pink tinges, rarely without, drying Light Ochraceous-Buff (XV15'd), Ochraceous Tawny (XV15'i), Ochraceous Salmon (XV13'b), rarely Mahogany (II7k). Ectal excipulum of textura angularis, cells globose when fresh or rehydrated, surface cells in chains which dry to form agglutinated fascicles, up to 100 µm long, each chain made of vesiculose or ovoid cells 10-15 µm wide, densely encrusted with irregular-shaped, yellowbrown pigmented Ca-ox granules. Subhymenium of textura intricata, hyphae with pale yellow or pale golden granulate inclusion, visible as a dark yellowish layer. Medullary excipulum of textura intricata, mostly hyaline with no encrustation or inclusion, or rarely appearing pale yellow with hyphae with pale golden inclusion. Ascospores ellipsoid to narrowly ellipsoid, widest at middle, mostly $12.0-15.0 \times 6.0-7.5$ (-8.0) μ m, 1.73 < Q < 2.00, av. 1.92, (n=9), rarely, [K(M)155461] as small as $10.5-13.3 \times 5.5-7.0 \mu m$, 1.75 < Q < 2.10, or [K(M)157354] (10–) 11.0–12.0 × 5.5–6.0 (–6.5) µm. Paraphyses not or only slightly swollen to 4 µm at apices, 2.5-3 µm wide at middle, mostly with no inclusion, rarely with pale golden granulate inclusion. UV reactions when dry: outer surface constantly dark under 254 nm or 365 nm, Prout's Brown (XV15'm) or Dresden Brown (XV17'k), although Nannfeldt (1966) described the reflection of the excipulum as 'characteristic golden brown'. Hymenium contrastingly pale, Pale Ochraceous-buff (XV15'f) or Light Ochraceous-buff (XV15'd) under 254 nm, whitish, Light Buff (XV17'f) or Light Ochraceous-Buff (XV15'd) under 365 nm. Encrustation of basal mycelium: small yellow crystals at places, pale yellow exudate when KOH

Distribution outside Britain: Scandinavian countries, Italy, USA (OLARIAGA *et al..*, 2015), Iran (BAHRAM *et al..*, 2012). Based on morphology, apparently widespread in Europe (REHM, 1894; ECKBLAD, 1968), and tentatively reported from Japan (IMAZEKI *et al..*, 1988; OTANI, 1989), and China (Cao *et al..*, 1990). A report from Mexico (RAYMUNDO *et al..*, 2019, Fig. 10E) is rejected, as the text (*op. cit.:* 22) gives the ascus as having an amyloid apex, which could not possibly refer to an *Otidea*.

Otidea concinna clade

4.-8 *Otidea caeruleopruinosa* Harmaja, *Karstenia*, 48: 37 (2009). Reported here for the first time from Britain.

Specimen: ENGLAND, Middlesex, Hampstead Heath, under *Quercus robur* and *Tilia* sp., 29 Sep. 2014, Overall, K(M)194835.

Specimen based on morphology only: ENGLAND, North-east Yorkshire, Thornton le Dale, 10 Sep. 1960, Sledge, via herb W.G. Graddon no.1536, K(M)137477.

Notes: The ITS sequence of K(M)194835 is identical to the Finnish holotype except with 3 gaps in 600 bases. Morphologically, the collection differs slightly from the holotype, in which the excipular colour was 'pale dirty brown' to 'pale brown or pale greyish brown when faded', with dark blue minute warts (HARMAJA, 2009). In K(M)194835 the excipulum was white when fresh, due to a dense covering of hyaline outgrowths, or hairs, comprising chains of 10-15 cells, up to 200 µm long. In the macro-photographs the receptacle shows a hint of blue, but not when the hairs were viewed under the microscope. It was collected under Tilia sp. and Quercus robur, whereas other European collections were from under Quercus robur and Corylus avellana, with Betula sp. and Buxus sempervirens also mentioned, or more generally Fagaceae hosts suggested. We failed to obtain a DNA sequence from K(M)137477 but the specimen was identified morphologically from Graddon's notes and micro-drawing (at the archive, RBG, Kew).

A photograph published by Van Vooren *et al.*. (2011) shows a Spanish collection MT10082601, the sequence of which was used by OLARIAGA *et al.*. (*op. cit.*). British specimens are morphologically in accordance with this collection, except that the ectal excipular hairs are much longer, leading to white appearance of the receptacle.

This species is characterised by the white appearance of the receptacle, small ascospores under 12 μ m long, broadest at middle, and clavate or subcapitate paraphyses. A dried specimen would resemble that of *O. alutacea*, but should be distinguished by warm

salmon colour when dry, and pigmented excipular cells covered with unencrusted outgrowths.

Species description: Apothecia solitary or in small clusters, narrowly ear-shaped, then cup-shaped, round truncate, $4-5\,\mathrm{cm}$ tall, 2-3 cm wide. Outer surface almost white, densely covered with white long hairs, some forming warts, surface appearing mealy white, finely scurfy, drying Pale Ochraceous-Salmon (XV13'f), the hymenium Pale Ochraceous-Buff (XC15'f), drying Pale Ochraceous-Salmon or Pale Drab-Gray (XLVI17""f). Ectal excipulum of textura prismatica, as long chains of up to 240 µm, made of ovoid or vesiculose cells, 10 µm wide, some of which form agglutinated fascicles, not encrusted with crystals, outgrowing from a solid excipular layer of textura angularis. In the latter layer, cells are globose when rehydrated, cell walls pale yellow, sparsely encrusted with pale golden pigments, surface covered with outgrowths in chains up to 240 µm long, composed of round or vesiculose cells, c. 10 µm wide, some of which form agglutinated fascicles, not encrusted with crystals. Subhymenium of textura intricata, pale yellow. Medullary excipulum of textura intricata, pale yellow. Paraphyses clavate to subcapitate, hyaline, slightly swollen at or gradually swollen towards apices up to (4.5–) 6–7 μ m. Ascospores ellipsoid, 10.0–12.0 (–12.5) \times 6.0– 6.5 μ m, 1.82<Q<2.00, av. 1.86 (n=30). Asci 150–180 \times 9–10 μ m. UV reactions when dry: outer surface Cartridge Buff (XXX19"f) under 254 nm and 365 nm, hymenium Pale Smoke Gray (XLVI21""f) under 254 nm and 365 nm. Encrustation of basal mycelium: small pale yellow crystals, only in places, pale yellow exudate when KOH added.

Distribution outside Britain: Known from Finland, Sweden, Spain (OLARIAGA *et al..*, 2015; VAN VOOREN *et al..*, 2011) and Italy (CARBONE & BOCCARDO, in press).

4.-9 Otidea concinna (Pers.) Sacc., *Syll. fung.*, 8: 96 (1889). Basionym: *Peziza concinna* Pers., *Mycol. eur.*, 1: 222 (1821).

Names used by British authors (misapplications):

Otidea cantharella (Fr.) Quél., Enchir. fung.: 275 (1886).

Flavoscypha cantharella (Fr.) Harmaja, sensu Harmaja, Karstenia, 14: 107 (1974).

History of British usage of the name: HARMAJA (1974) applied his then new combination, Flavoscypha cantharella, to an Otidea which had until then been known by British authors as O. concinna (Pers.) Sacc. (Ramsbottom & Balfour-Browne, 1951; Dennis, 1960, 1968). This misapplication led to Cannon et al.. (1985) placing O. concinna and O. cantharella into synonymy. The Flavoscypha combination was adopted by Dennis (1978, 1981) and by subsequent British authors. However, Harmaja (2009) later noted Bresadola's interpretation of Peziza cantharella Fr. (Bresadola, 1900, p. 102, pl. 214; 1933, pl. 1227), and thought that O. cantharella should apply to a larger-spored, pale coloured species (spores $19-21 \times 9-12 \mu m$) and not to the species described here. Olariaga et al.. (2015) studied Swedish material of Peziza cantharella Fr. from Fries' herbarium, confirmed Harmaja's conclusion, and selected a neotype for O. concinna. True O. cantharella has not been found in Britain. 15 British specimens previously held at K as O. cantharella have been redetermined as O. concinna (12), O. onotica (2) and O. formicarum (1).

Selected specimens: ENGLAND, Middlesex, Bushy Park, 13 Sep. 1987, Spooner *et al.*, K(M)119613; Laleham, under *Quercus cerris*, 15 Oct. 2016, Parslow, K(M)237113; North Northumberland, Rothbury (near), under *Fagus sylvatica*, 7 Sep. 2001, Spooner & Henrici, K(M)124736. Scotland, Mid Perthshire, Killiecrankie, under *Fagus sylvatica*, Sep. 1988, Robinson, K(M)119620.

Selected British illustrations: DENNIS (1968, pl. 5 D painted from K(M)119609; in 1978 and 1981 editions pl. 8 E, misprinted as D at the bottom of the plate, and in the text p. 27 as pl. 7, D, also an error); R. PHILLIPS (1981: 271, photograph, of K(M)119612).

Notes: OLARIAGA *et al.*. (*op. cit.*) selected one of Schaeffer's illustrations (Schaeffer, 1763, pl. 150, f. 1, cited by Persoon, 1822) as the lectotype, and designated a Swedish epitype, KH 09. 183 (S). British sequences clustered with the epitype, strongly supported. Of 15 *O. concinna* collections, ten were collected at woodland edge or in



Fig. 4 – *Otidea caeruleopruinosa*; a: K(M)194835, a part, when fresh after collection, showing a hint of Pale Ochraceous-Salmon colour in mature hymenia. Photograph A. Overall; b: England, Middlesex, Hampstead Heath, under *Quercus robur* and *Tilia* sp., 29 Sep. 2014, Overall, K(M)194835. Scale bar = 10 μ m; c: K(M)194835, scale bar = 10 mm; d: K(M)194835, a part, *in situ*. Photograph A. Overall.

wooded parks or gardens. They are from 14 localities, widespread in Britain. Four are associated with *Quercus* spp., four with *Fagus sylvatica*. However, only two collections (vouchered) are from the 21st century, so this species cannot be described as 'common'.

A confusion arose from what can now be seen as errors by DENNIS, in his ground-breaking *British Ascomycetes* (1968) and its later editions (1978, 1981). His illustration of *O. concinna* (1968, pl. 5, D) was of K(M)119609 (Scarborough, under *Fagaceae*, Rimington, 28 Aug. 1949, *O. concinna*), identified from data on his original drawing which is identical to his plate 5 D (not reproduced here due to copyright issues). This illustration was later renamed *Flavoscypha can-*

tharella (1978 & 1981, pl. 8, E, erroneously marked D in the legend). In addition, Dennis' description in the text (Inverness-shire, Aviemore, under *Pseudotsuga*, 26 Sep. 1950) was erroneous, and does not refer to K(M)119609; the only *Otidea* at K which this data refers to is K(M)155410, the possible origin of his *O. phlebophora* drawing (DENNIS, *op. cit.*, pl. 8 D, erroneously E in the legend). Further, and more confusingly, this illustration was subsequently referred to *O. minor* by Olariaga *et al.*. (*op. cit.*: 219). In the present study, the relevant specimen, K(M)155410, has been redetermined as *O. formicarum* (see later). The said original drawing by Dennis of K(M)155410 is shown below in relation to *O. formicarum* (with the relevant part



Fig. 5 – *Otidea concinna*; a: England, Middlesex, Bushy Park, 13 Sep. 1987, Spooner *et al..*, K(M)119613. Scale bar $(a-c) = 10 \mu m$; b: Scotland, Mid Perthshire, Killiecrankie, under *Fagus sylvatica*, Sep. 1988, Robinson, K(M)119620; c: England, North Northumberland, Rothbury (near), under *Fagus sylvatica*, 7 Sep. 2001, Spooner & Henrici, K(M)124736; d: K(M)124736. Scale bar $(d-e) = 10 \mu m$; e: England, Laleham, under *Quercus cerris*, 15 Oct. 2016, Parslow, K(M)237113; f: K(M)237113, a part, when fresh after collection; g: K(M)237113, *in situ*.

of the image digitally 'blurred', so as not to infringe publisher's copyright).

O. concinna has sizeable apothecia, bright sulphur yellow above, with a white, well rooted base, drying warm tawny colour. Under UV light the dark receptacle contrasts strongly with the delicate mustard- or pale green yellow hymenium.

Species description: Apothecia in small clusters, broad earshaped, later truncate, up to 4.5 cm tall, 5 cm wide, Citrine Yellow (XVI23'b), whitish below, drying Ochraceous Tawny (XV15i') or Yellow Ocher (XV17'), surface granulate or scurfy. Hymenial colour Cream (XV19'f) drying Warm Buff (XV17'd) or Antimony Yellow (XV17'b). Ectal excipulum of textura prismatica, long chains outgrowing from a layer of textura angularis, cells globose when fresh or rehydrated, encrusted with yellow or pale-golden pigmented Ca-ox crystals. Subhymenium of textura intricata, hyaline or very pale yellow. Medullary excipulum of textura intricata, hyaline or very pale yellow. Paraphyses swollen or slightly swollen to 4–6 (8) μm wide at apices, subcapitate, lacking pigmentation nor inclusion. Ascospores ellipsoid, (10.0–) 10.5–12.5 \times 5.5–6.5 μ m, 1.70<Q<2.05, av. 1.87 (n=40). Asci 150–180 \times 9–10 µm. UV reactions when dry: outer surface Dresden Brown (XV17'k) or Mummy Brown (XV17'm) under 254 nm and 365 nm, hymenium Mustard Yellow (XV19'b), Naples Yellow (XVI19'd) or Massicot Yellow (XVI21'f) under 254 nm, Naphthalene Yellow (XVI23'f) under 365 nm. Encrustation of basal mycelium pale yellow pigmented, mostly yellow when KOH added (but not observed in K(M)119613).

Distribution outside Britain: Known from Scandinavian countries and Spain (Olariaga *et al.., op. cit.*). Reported based on morphology from Switzerland (Breitenbach & Kränzlin, 1984), France (Mornand & Cortecuisse, 2005), Italy (Medardi, 2006), Macedonia (Kajevska *et al..*, 2013), China (Cao *et al..*, 1990; Mao, 2000; Zhuang, 2005; Li *et al..*, 2015).

4.-10 *Otidea flavidobrunneola* Harmaja, *Karstenia*, 48: 38 (2009). Reported here for the first time from Britain.

Specimens: ENGLAND, Middlesex, Hampstead Heath, 29 Jul. 1973, anon., K(M)155407; South Essex, Little Baddow, under *Quercus robur*, 29 Sep. 2010, Gregory, K(M)196021.

Notes: The species description below has been supplemented with Harmaja's description from the Finnish holotype and information from photographs by Olariaga *et al.*. (*op. cit.*: 218). Harmaja (2009) suggested a macro-morphological similarity to *O. bufonia*, and indicated (the key, p. 41) the receptacle to be brown and the

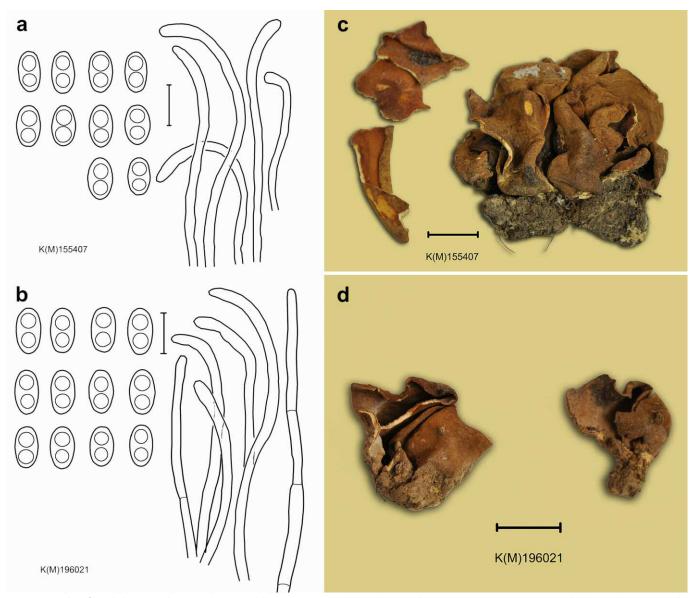


Fig. 6 – Otidea flavidobrunneola; a: England, Middlesex, Hampstead Heath, 29 Jul. 1973, anon. K(M)155407. Scale bar (a–b) = 10 μ m; b: Little Baddow, under Quercus robur, 29 Sep. 2010, Gregory, K(M)196021; c: K(M)155407, dry receptacle Buckthorn Brown, hymenium Yellow Ocher. Scale bar (c–d) = 10 mm; d: K(M)196021, dry receptacle Dresden Brown, hymenium Cinnamon Brown, in contrast to buff colour when fresh.

hymenium yellowish, as confirmed in K(M)196021 when fresh. For K(M)155407, relatively early fruition in the year has been noted.

Species description: Apothecia gregarious, or in small clusters. The receptacle of K(M)196021 was recorded as 'between buff and luteolus' when fresh, which should refer to Warm Buff (XV17'd), then drying Dresden Brown XV17'k) or Buckthorn Brown (XV17'i). Hymenium paler yellowish, or almost white when fresh, drying Cinnamon Brown (XV15'k) or Yellow Ocher (XV17'). Ectal excipulum: outer layer of textura prismatica, in chains up to 120 μm long, encrusted with brown to yellowish brown sizeable crystals of 4–7 µm diameter, inner later of textura angularis but not well defined, cells subglobose when rehydrated, encrusted with brown pigmented crystals. Yellow exudates observed in 10% KOH. Subhymenium of textura intricata, hyaline. Medullary excipulum of textura intricata, tightly packed, 600 µm thick, hyaline, with small amount of yellow granules in places. Paraphyses not swollen at apices, slightly curved, no pigmentation. Ascospores $9.5-11.5 \times 5.5-6.0 (-6.5) \mu m$, 1.67 < Q < 1.88, av. 1.85 (n=42). Asci 150–160 \times 9–10 μ m. UV reactions when dry: outer surface Mummy Brown (XV17'm) under 254 nm, Mummy Brown or Clay Colour (XXIX17") under 365 nm, hymenium Isabella Color (XXX19"i) under 254 nm, Isabella Color or Chamois (XXX19"b) under 365 nm. Encrustation of basal mycelium hyaline, yellow when KOH added.

Distribution outside Britain: Scandinavian countries (OLARIAGA *et al.., op. cit.*), Italy (CARBONE *et al..,* 2019b) and Russia (SVETASHEVA *et al..,* 2016). Reported online from Czech Republic in 2016 (www.ascofrance.com/forum/45864/otidea-sp).

4.-11 Otidea phlebophora (Berk. & Broome) Sacc., *Syll. fung.*, 8, 97 (1889).

Basionym: *Peziza phlebophora* Berk. & Broome, *Ann. Mag. nat. Hist., Ser. 3*, 18: 122 (1866).

Synonym used by British authors:

Flavoscypha phlebophora (Berk. & Broome) Harmaja, Karstenia, 14: 107 (1974)

History of British usage of the name: As *Peziza* in various publications, including Cooke (1879, fig. 217) and Phillips (1887). Massee (1895) and Dennis (1968) adopted an Otidea combination (as 'plebophora', a typographic error), whereas the latter subsequently took to Harmaja's Flavoscypha combination (Dennis, 1978, 1981). In the 1866 protologue, two collections were mentioned, one by Berkeley from King's Cliff, Northamptonshire, and another by Broome from Brislington, North Somerset. At K, there is one collection which refers to the former [1853, Berkeley, K(M)144046], and three packets which refer to the latter, one of which was received directly from Broome [16 Sep. 1853, Broome, K(M)144045], and another probably from Berkeley as it is marked with Berkeley's handwriting [Sep. 1853, Broome, K(M)194582]. The latter two are morphologically identical and represent isosyntypes. Another Brislington collection, K(M)194584, had initially been thought to be an isosyntype, but being ex Herb. W. Phillips and without date, it cannot be automatically considered a type. Harmaja had previously examined K(M)144046, and annotated it as lectotype of O. phlebophora (as Flavoscypha phlebophora), though failed to publish the lectotypification (Harmaja, 1974). Olariaga et al.. (op. cit.) validly lectotypified this species with K(M)144045, and stated (ibid.: 223) that the lectotype conforms morphologically to current usage of the name.

British types: England, North Somerset, Brislington, 16 Sep. 1853, anon, ex Herb. C.E. Broome, K(M)144045, lectotype designated by OLARIAGA *et al.*. (2015: 222), Mycobank MBT178087, Index Fungorum Identifier 590593; *ibid.*, Brislington, The Beeches, Sep. 1853, Broome, K(M)194582, syntype; Northamptonshire, King's Cliff, 1853, Berkeley, K(M)144046, syntype, but see the notes above.

Specimens: ENGLAND, Durham, Darlington, Holy Trinity Church, 29 Nov. 1995, on soil on mossy lawn, Legg, K(M)33068; North Somerset, Brislington, sine datum, anon., ex Herb. W. Phillips, K(M)194584; South Devon, Lincombe Slopes, under *Quercus ilex*, 18 Dec. 2006, Roberts, K(M)143475.

Selected British Illustrations: Berkeley & Broome (1866, pl. 3, 9); Cooke (1879, pl. 55, fig. 217, an illustration of K(M)194584).

DENNIS (1978, 1981, Pl. 8, D, misprinted as E on the legend and on p. 26, as *Flavoscypha phlebophora*) is unreliable as a representation of this species as it may have been derived from K(M)155410, which is *O. formicarum*.

Notes: As explained below and shown on sub-micro drawings (Fig. 7a, 7b), we consider the lectotype conspecific and almost identical to an English collection, K(M)33068, from which an ITS sequence was obtained and used for DNA analysis by Olariaga *et al.*. (*op. cit.*) and in this study. When analysed with online BLAST tool, the ITS sequence obtained from K(M)33068 (GenBank no. EU784392) is 99.2 % identical (at query coverage 99%, 555 bases) to those from the Scandinavian vouchers assigned by Olariaga *et al.*. to *O. phlebophora*. The difference was only due to four gaps, two of which are outside the ITS1 range. At present, current assignation of molecular data to this species, as in Olariaga *et al.*. (*op. cit.*) and in the current study, supports the latest lectotypification.

Examination of another syntype, K(M)144046 from King's Cliff, revealed two apothecia with larger ascospores (11.0–13.5 \times 5.5–6.5 μ m) than the lectotype (see below), and with paraphyses subclavate rather than capitate or subcapitate as in the lectotype. They may belong to another taxon, or intraspecific taxon. Our observation contradicts with Olariaga's note (undated) attached to the specimen in spore sizes and other details, so that it is possible that the collection is mixed.

British *O. phlebophora* collections are characterised by small yellow or ochre apothecia, venose underneath, relatively small spores which rarely exceed 12.5 μ m long, and capitate or subcapitate paraphyses.

Species description: Apothecia solitary or in small clusters, gregarious, 1-3 cm wide, 1-2.5 cm tall. Receptacle colour 'yellow or brownish' in the protologue, 'yellow' in K(M)33068, Ivory Yellow (XXX21"f) in K(M)143475; when dry becoming varying shades and mixtures of Honey Yellow (XXX19"), Clay Color (XXIX 17") or Cinnamon (XXIX15"). Hymenium Ivory in K(M)143475, drying Tawny Olive (XXIX17"i), Cream Buff (XXX19"d) and Cartridge Buff (XXX19"f). All receptacles show anastomosing venose patterns below when dry, although those pasted on the fungarium sheet could not be examined, and in small apothecia of under 5 mm in diameter the pattern is not apparent. Ectal excipulum of textura prismatica, cells elongated cylindrical with clavate terminals, cell walls encrusted abundantly with yellow- or golden-yellow pigmented granules. Subhymenium with pale yellow or golden yellow pigments on cell walls, inclusion hyaline. Medullary excipulum with minute yellow granules on cell walls, inclusions hyaline or pale yellow. Paraphyses with yellow inclusion in the lectotype K(M)33068, hyaline in K(M)143475, 2–3 μm at middle, swollen at apices to 4–8 μm, capitate or subcapitate, moniliform or submoniliform at base. Ascospores ellipsoid to ellipso-fusoid, in the lectotype (9.5–) $10.0-12.5 \times 5.0-$ 6.5 μm, 1.90<Q<1.93, av. 1.91 (n=24), in K(M)33068, (9.5–) 10.0–11.5 $(-12) \times 5.0$ -6.0 μ m, 1.90<Q<2.00, av. 1.93 (n=20), in K(M)143475, $8.5{-}10.5 \times 5.0{-}5.5~\mu m$, 1.70<Q<2.10, av. 1.90 (n=24). Asci in all collections 150–155 \times 9–10 μm . UV reactions when dry: outer surface Isabella Color (XXX19"i) in K(M)33068, or Chamois (XXX19"b) to Isabella Color (XXX19'i) in the lectotype, under 254 and 365 nm, hymenium Cartridge Buff (XXX19"f) in K(M)33068, Cartridge Buff (XXX19"f) or Honey Yellow (XXX21'f) in the lectotype, under 254 and 365 nm. Encrustation of basal mycelium hyaline, no reaction to KOH.

Distribution outside Britain: Scandinavian countries (Olariaga *et al.., loc. cit.*), reported from Germany (Häffner, 1994), Italy (Medardi, 2006) and France (Mornand & Courtecuisse, 2005).

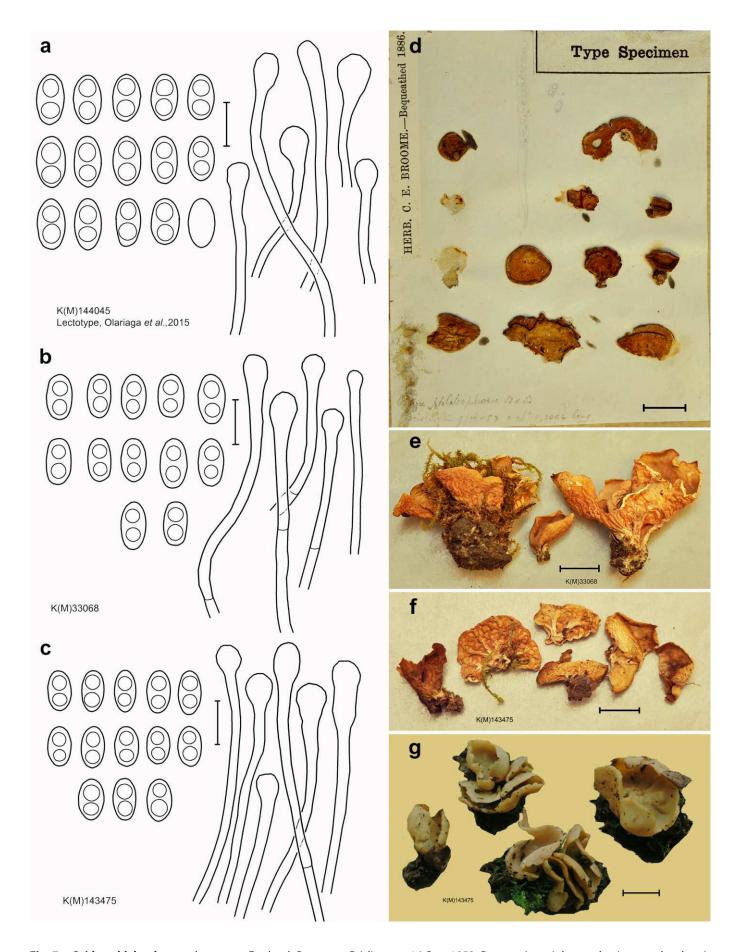


Fig. 7 – *Otidea phlebophora*; a: lectotype, England, Somerset, Brislington, 16 Sep. 1853, Broome (top right apothecium on the sheet), K(M)144045. Scale bar $(a-c) = 10 \mu m$; b: England, Durham, Darlington Holy Trinity Church, 29 Nov. 1995, Legg, K(M)33068; c: England, South Devon, Lincombe Slopes, 18 Dec. 2006, Roberts, K(M)143475; d: lectotype, K(M)144045. Scale bar $(d-g) = 10 \mu m$; e: K(M)33068, considered conspecific to the lectotype; f: K(M)143475; g: K(M)143475, after collection when still fresh. Photograph P. Roberts. The background colour has been changed from dark blue to a neutral colour with Adobe Photoshop CS6 software.

4.-12 *Otidea minor* (Boud.) Olariaga & K. Hansen, *Persoonia*, 35: 219 (2015).

Confirmed here as a British species.

Basionym: Otidea cantharella var. minor Boud., Icon. mycol., livr. 23, 411, pl. 326 (1909).

History of British usage of the name: In 1977, R. Watling sent one Otidea to W.D. Graddon, for identification. Graddon's research note (at the archive of RBG, Kew) indicates that he initially considered O. kauffmanii (synonym O. rainierensis, not British) but later named it O. cantharella var. minor Boud, and presented it to K [K(M)41748]. Although this application was never published, the name was copied by the British Mycological Society's online database, the Fungal Record Database of Britain and Ireland (hereafter FRDBI) and by the British National Biodiversity Network (NBN Atlas). Meanwhile, Olariaga et al.. (2015), raised Boudier's variety to the rank of species based on their multigene analysis of the genus (op. cit.: 173-174), during which Harmaja's 'O. subconcinna' (HARMAJA, 2009, not validly published) was proved to be of this species. During the current study, K(M)41748 was initially grouped with morphologically similar specimens previously named O. phlebophora. ITS sequences were extracted and three of them clustered with European sequences of O. minor used by Olariaga et al.. (loc. cit.), hence confirmation of this species in Britain. The two Scottish specimens cited below deviate slightly from K(M)41748 and may represent a lineage within the species.

Specimens: ENGLAND, West Lancashire, Silverdale, under *Larix* sp. Sep. 1977, Graddon, K(M)41748. SCOTLAND, Mid Perthshire, Killiecrankie, near *Fagus sylvatica*, 8 Sep. 1993, Robinson, K(M)24355; Killiecrankie, near *Fagus sylvatica*, 2 Sep. 1997, Krueger, K(M)55019.

Notes: OLARIAGA *et al.*. (*loc. cit.*) designated BOUDIER's plate 326 as lectotype of *O. cantharella* var. *minor* and hence of *O. minor*. The macro-characters of this species are shared with *O. phlebophora*, including yellow colour (although said to be in different tones, HARMAJA, 2009), small truncate apothecia, and receptacles

venose-patterned below. However, *O. minor* can be distinguished under the microscope relatively easily from *O. phlebophora*, due to its longer and relatively narrower spores, and paraphyses mostly slightly curved and cylindrical (instead of straight, capitate, or subcapitate), with refractive inclusions. We note that the latter character, noted by Olariaga *et al.*. (*loc. cit.*) in fresh collections, remains apparent when dried and rehydrated. A similar, yellow receptacle will be found in *O. formicarum*, for which see later.

Species description: Apothecia gregarious or solitary, 'citrine yellow' outside, hymenium 'yellow or yellowish gray' (Olariaga et al.., loc. cit.; HARMAJA, 2009: 47). Ectal excipulum of textura angularis, cells globose when rehydrated, loosely packed, with short outgrowths, encrusted moderately densely or densely (as in K(M)41748) with dark yellow brown pigmented crystals. Subhymenium of textura intricata, hyaline. Medullary excipulum of textura intricata, hyaline. Paraphyses when rehydrated with pale yellow pigmentation on cell walls, either in places or entirely, refractive inclusions either at apices or entirely, slightly curved above or sometimes straight, 2.5-4 µm wide at middle, not or only slightly swollen at apices. Ascospores ellipso-fusoid, 12.0–14.0 (–14.5) \times (5.0–) 5.5–6.5 μ m, 2.02<Q<2.40, av. 2.21 (n=40). Asci 190–200 \times 11 μ m. UV reactions when dry: outer surface mummy Brown (XV17'm) or Olive Brown (XL17"k) under 254 nm, Prout's Brown (XV15'm) under 365 nm, hymenium Mustard Yellow (XVI19'b) or Light Chalcedony Yellow (XVII 25'd) under 254 nm, Naphthalene Yellow (XVI23'f) or Pale Chalcedony Yellow (XVII 25'f) under 365 nm. Encrustation of basal mycelium hyaline, no reaction to KOH.

Distribution outside Britain: Scandinavian countries and Italy (OLARIAGA *et al..*, *op. cit.*), reported from Germany (HÄFFNER, 1994), France (BOUDIER, 1908c; VAN VOOREN, 2017), and online from Czech Republic (www.ascofrance.com/forum/49208/otidea-cf-minor). We note that, in the latter report, the sub-micro details of the specimen discussed differed from our observations of *O. minor*, in the spore lengths and Q, and in shape of paraphyses.

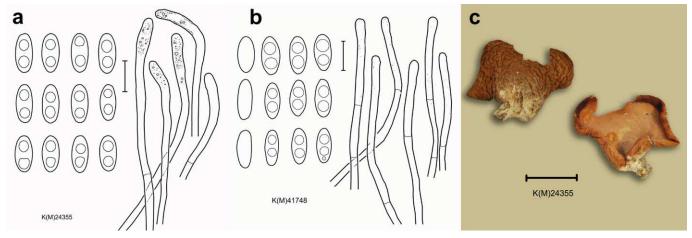


Fig. 8 – *Otidea minor*; a: Scotland, Mid Perthshire, Killiecrankie, near *Fagus sylvatica*, 8 Sep. 1993, Robinson, K(M)24355. Scale bar (a–b) = $10 \mu m$; b: England, West Lancashire, Silverdale, under *Larix* sp. Sep. 1977, Graddon, K(M)41748; c: K(M)24355. Only one apothecium remains, so that an image of receptacle (left) and that of hymenium (right) are combined in one with Adobe Photoshop CS6 software. Scale bar = $10 \mu m$.

Otidea leporina clade

4.-13 *Otidea leporina* (Batsch) Fuckel, *Jahrb. Nassauischen Vereins Naturk.*, 23-24: 329 (1870).

Basionym: Peziza leporina Batsch, Elench. fung., 1: 117 (1783).

History of British usage of the name: Peziza leporina, the basionym of Otidea leporina, has been variously interpreted, and was once applied to Wynnella (Helvella) silvicola (Franchi et al.., 1999), a species now known as Midotis lingua Fr., for which see Hansen et al.. (2019), an application rejected by Parslow & Spooner (2009) and Olariaga et al.. (2015: 187). The latter (ibid.: 185) lectotypified Peziza (Otidea) leporina with Schaeffer's pl. 156 (1763), and selected a

Swedish epitype, thus stabilising the usage of the name. As already explained above (see 3), of 87 collections at K previously named *O. leporina*, mostly from the 19th- and some from the 20th-century, most have been redetermined, as follows: *O. alutacea* and related unnamed taxa (26); *O. parvispora* (1); *O. bufonia* (20); *O. onotica* (13); *O. concinna* (4); *O. formicarum* (2); *O. tuomikoskii* (2); *O. phlebophora* (1); *O. nannfeldtii* (1); *Sowerbyella radiculata* var. *petaloidea* (Cooke & W. Phillips) Y.J. Yao & Spooner (1); *Peziza badia* Pers. (1); *Midotis lingua* (1). Ten collections being immature, burnt or degraded, and which failed to produce a DNA sequence, could not be positively identified but four are likely to be *O. phlebophora*, six *O. onotica*. Hence, only

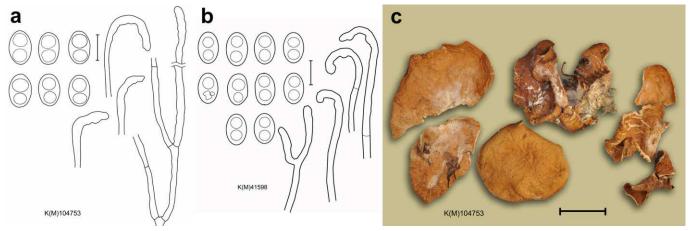


Fig. 9 – *Otidea leporina*; a: Scotland, Easterness, Cairngorms, Glenmore Forest Park, under *Picea abies*, 18 Oct. 2002, Emmett, K(M)104753. Scale bar (a–b) = 10 μm; b: Scotland, Angus, Edzell, under *Pinus* sp., Sep. 1953, Henderson, K(M)41598; c: K(M)104753. Scale bar = 10 mm.

four have retained the original name. One other, previously as *O. alutacea*, has been redetermined and confirmed as *O. leporina* (BROCK *et al..*, 2009).

Specimen: Scotland, Easterness, Cairngorms, Glenmore Forest Park, under *Picea abies*, 18 Oct. 2002, Emmett, K(M)104753.

Specimens based on morphology only: ENGLAND, Shropshire, Tibberton Firs, 1874, anon, ex herb. W. Phillips, K(M)155514; West Norfolk, King's Lynn, Sep. 1872, Plowright & Plowright, K(M)155511. Scotland, Angus, Edzell, under *Pinus* sp., Sep. 1953, Henderson, K(M)41598.

Notes: According to OLARIAGA *et al.*. (*loc. cit.*), *O. leporina* is the most common *Otidea* species in boreal coniferous forest in Europe. In Britain, it seems to be one of the rarest or least often collected, most likely due to the relative lack of coniferous habitat in the south-east, and may have been overlooked in the north where coniferous forest is extensive. This species is easily recognised with medium to small apothecia, brownish receptacle, drying ochre to medium brown, not dark, not yellow, broad spores (Q av. 1.65) of 12-15 μ m in length, and mostly notched or lobed paraphyses.

Species description: Apothecia gregarious, some in small clusters, British collections only up to 3 cm tall when fresh (up to 5 cm in Olariaga et al.., op. cit.: 185), hygrophanous, 'ochre brown' fide OLARIAGA et al.. (loc. cit.), granulate or smooth when dry, drying Tawny (XV13'i) or Ochraceous Tawny (XV15'd), hymenium Ochraceous-Buff (XV15'b), drying Ochraceous-Buff, Cinnamon Brown (XV15f') or Russet (XV13'k). Ectal excipulum with surface cells densely encrusted with yellowish brown pigmented Ca-ox crystals. Medullary excipulum of textura intricata, hyaline, or with very pale yellow pigments on cell walls. Subhymenium of textura intricata, pale yellow. Paraphyses hyaline or very pale yellow, apices not or only slightly swollen, 2-3.5 µm wide at middle, 3-4 or 5-6 µm near apices, curved, with a small protuberance or notched at or near apices, rarely branched. Ascospores broad ellipsoid, 12.0–14.5 (–15.0) × 7.5– 9.2 (-9.5) μ m, 1.57<Q<1.73, av. 1.65 (n=17). Asci 190–200 × 9–10 μ m. UV reactions when dry: outer surface Ochraceous Tawny (XV15'i) or Chamois (XXX19'b) under 254 and 365 nm, hymenium Light Ochraceous-Buff (XV15'd) or Cream Buff (XXX19"d) under 254 nm, Light Buff (XV17'f), Pale Ochraceous-Buff (XV15'f) or Cream Buff under 365 nm. Encrustation of basal mycelium: small yellow crystals in places, no colour reaction in KOH.

Distribution outside Britain: Widespread in Europe in boreal coniferous zone (OLARIAGA *et al..*, 2015).

Otidea formicarum clade

4.-14 *Otidea formicarum* Harmaja, *Karstenia*, 15: 31 (1976). Reported here for the first time from Britain.

Specimen: SCOTLAND, Easterness (East-Inverness-shire), Cairngorms, Aviemore, road to Kincraig, under *Pseudotsuga* sp., 26 Sep. 1950, Dennis, K(M)155410.

Selected specimen based on morphology only: England, Surrey, Brookwood Cemetery, under *Picea* sp., 22 Dec. 2002, Brown, K(M)106912.

Selected British Illustrations: As explained in 4.-9, it is probable that the pl. 8 D in Dennis (1978 and 1981, but in the legend and in the text as 8 E, an error) was based on K(M)155410. Dennis' original drawing is presented as Fig. 10b; the first apothecium on the left, suspected to be the origin of his illustration, has been blurred using Adobe Photoshop CS6 software, so that this figure would not infringe the copyright.

Notes: The epithet reflects the fact that the Finnish holotype, from spruce forest, was found on an anthill. British collections are indeed on conifers, *Pseudotsuga* and *Picea*, though no relationship with ants was specifically recorded for them. This species should be noted for its yellow receptacle and hymenium, small broad spores, and strongly curved, often notched, paraphyses. Also notable are the yellow-pigmented medullary excipular hyphal cells, and the subhymenium which has inclusions of golden granules, similar to those of *O. phlebophora*. The yellowish receptacle and lack of refractive guttules in the paraphyses are not in accordance with the description by Olariaga *et al.*. (*op. cit.*), so that there is evidently some morphological variation within the species.

Species description: Apothecia gregarious, or in clusters, earshaped to broad-funnel shaped, but not broadly truncate. Dennis's illustration suggests receptacle and hymenium to be bright Antimony Yellow (XV17'b), Yellow Ochre (XV17'), or Chamois (XXX19"b) when dry. Ectal excipulum of textura angularis, cells large globose when rehydrated, entire cell walls appearing as if yellow-pigmented or thick-walled because of presence of gelatinous 'sheath', slightly encrusted with golden yellow crystals, up to 10 µm in diameter. Medullary excipulum of textura intricata, yellow, cell walls yellowpigmented. Subhymenium of textura intricata, yellow, cell walls encrusted with golden granules. Paraphyses strongly curved, bent or hooked, mostly with a small protuberance, or notched, not or slightly swollen at apices. Ascospores broad ellipsoid, 9.5–11.0 \times 6.0-7.0 (-7.5) μ m, 1.47 < Q < 1.53, av. 1.53. Asci $120-160 \times 10-12$ μ m. UV reactions when dry: outer surface Chamois (XXX19"b) under 254 and 365 nm, hymenium Cream-Buff (XXX19"d) under 254 nm, Cartridge Buff (XXX19"f) under 365 nm. Encrustation of basal mycelium: small yellow crystals in K(M)155410, no colour reaction to KOH.

Distribution outside Britain: Scandinavian countries (OLARIAGA *et al.., op. cit.*), France (*ibid.*; VAN VOOREN, 2017). Reported online from Italy (M. Zugna, at http://www.ambmuggia.it/forum/topic/6676-otidea-formicarum/, which showed images of brown and ochre apothecia)

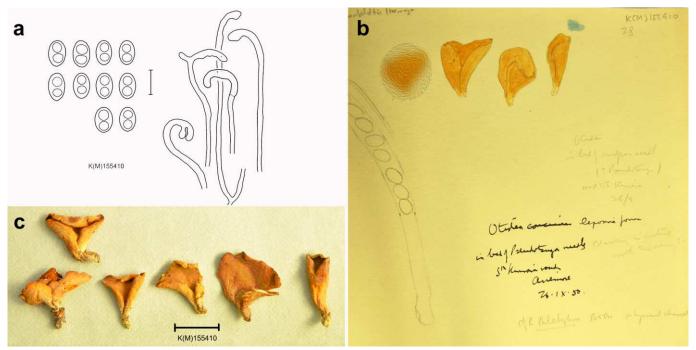


Fig. 10 – *Otidea formicarum*; a: Scotland, Easterness, Cairngorms, Aviemore, under *Pseudotsuga* sp., 26 Sep. 1950, Dennis, K(M)155410. Scale bar = $10 \mu m$; b: K(M)155410, illustration by Dennis, 1950. The top left apothecium which may have been the origin of Dennis's published illustration (1968, 5 D, 1978 & 1981, 8 E) is blurred using Adobe Photoshop CS6 software to protect the publisher's copyright; c: K(M)155410. Scale bar = $10 \mu m$.

4.-15 *O. nannfeldtii* Harmaja, *Karstenia*, 15: 31 (1976). Reported here for the first time from Britain.

Specimen: ENGLAND, South Lancashire, Formby, under *Pinus* sp., 27 Sep. 1946, Baker, K(M)155424.

Notes: Having examined the isotype of *O. nannfeldtii*, K(M)155124, a slide prepared from the holotype H6002902, we identified K(M)155424 as *O. nannfeldtii*, confirmed based on the ITS. This species is very similar to *O. formicarum*, to which name this collection was originally referred, except that (in British collections) the yellow-brown encrustation of the ectal excipulum is inclined to be more strongly brownish than that in *O. formicarum*. Paraphyses are also strongly curved as in *O. formicarum*; however, we did not see any apparent protuberance, as seen in *O. formicarum*.

Species description: Apothecia gregarious, receptacle recorded as 'brown' when fresh, no detail, European collections 'brown orange or pale brown, dried Ochraceous Tawny (XV15'i). Ectal excipulum of-textura angularis, cells globose when rehydrated, not in chains, some cell walls appearing as if thick-walled because of presence of gelatinous or thin golden 'sheath', encrusted with yellow-brown pigmented crystals, with irregular outgrowths agglutinated in places

and resembling warts. Medullary excipulum of *textura intricata*, yellow, cell walls yellow-pigmented. Subhymenium of *textura intricata*, yellow, cell walls encrusted with golden granules. Paraphyses curved, not swollen at apices, with pale yellow inclusion. Ascospores broad ellipsoid, (8.5–) 9.0–9.5 (–10.0) \times 5.5–6.0 (–6.5) μm , 1.54<Q<1.64, av. 1.53 (n=20). Asci 110–120 \times 7–9 μm . UV reactions when dry: outer surface Mummy Brown (XV17'm) under 254 nm, Buckthorn Brown (XV17'i) under 365 nm, hymenium Isabella Color (XXX19"i) under 254 nm, Chamois (XXX19"b) under 365 nm. Encrustation of basal mycelium slight in K(M)155424, no reaction to KOH.

Distribution outside Britain: Scandinavian countries, France, Italy, USA (OLARIAGA *et al..*, *op. cit.*).

Otidea tuomikoskii clade

4.-16 *O. tuomikoskii* Harmaja, *Karstenia*, 15: 30 (1976). Reported here for the first time from Britain.

Specimens: ENGLAND, South Wiltshire, Clanger Wood, under *Picea abies*, 10 Nov. 2012, Legon, K(M)237118. Scotland, Caithness, Dunnet Forest, under *Picea sitchensis*, 17 Sep. 2007, Savage, K(M)155378; East Perthshire, Blairgowrie, under *Picea* sp., 22 Sep. 2008, Wegner,

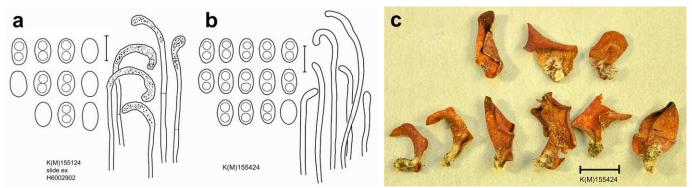


Fig. 11 – *Otidea nannfeldtii*; a: isotype K(M)155124, a slide made from the holotype, Finland, Ahvenanmaa, Lemland, Nåtö, 17 Sep. 1972, Haeggström, H6002902. Scale bar $(a-b) = 10 \mu m$; b: England, South Lancashire, Formby, under *Pinus* sp., 27 Sep. 1946, Baker, K(M)155424; c: K(M)155424. Scale bar = 10 mm.

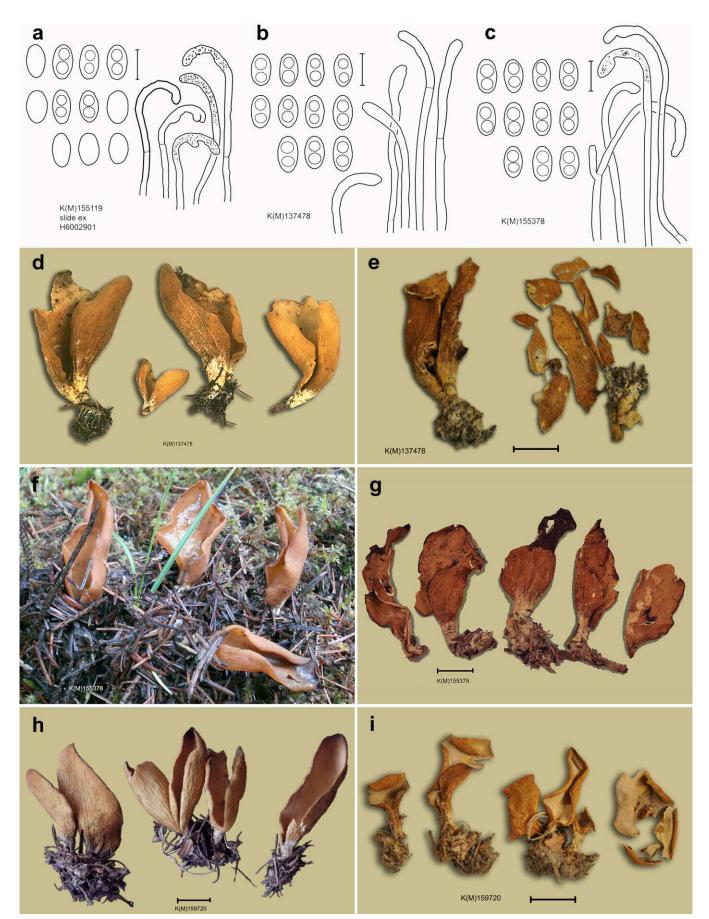


Fig. 12 – *Otidea tuomikoskii*; a: isotype, K(M)155119, a slide made of the holotype, Finland, Etelä-Häme, Lammi, Pappilankylä, in *Picea* needles on an anthill, 9 Sep. 1972, Tuomikoski, H6002901. Scale bar (a–c) = 10 μm; b: Wales, Anglesey, Newborough Warren, under *Picea* sp., 5 Oct. 1981, R. Brown, K(M)137478; c: Scotland, Caithness, Dunnet Forest, under *Picea sitchensis*, 17 Sep. 2007, Savage, K(M)155378; d: K(M)137478, photograph R. Brown, in the transparency collections (Kew Mycology), courtesy of the trustees of RBG, Kew. The background changed from dark blue to a neutral colour by Photoshop. Scale bar (d–i) = 10 mm; e: K(M)137478, hymenium dried Ochraceous Tawny; f: K(M)155378, *in situ*, photograph D. Savage; g: K(M)155378, hymenium dried Tawny; h: Scotland, East Perthshire, Blairgowrie, under *Picea* sp., 22 Sep. 2008, Wegner, K(M)159720. The background colour changed from dark blue to a neutral colour by Photoshop; i: K(M)159720, hymenium dried Light Buff.

K(M)159720. WALES, Anglesey, Newborough Warren, under *Picea* sp., 5 Oct. 1981, Brown, K(M)137478.

Specimens selected based on morphology only: Scotland, North Ebudes, Isles of Rhum, Loch Scresort, under *Picea* sp., 30 Aug. 1962, Dennis, K(M)155397. Wales, Carmarthenshire, Pembrey Forest, under conifers, 3 Oct. 1982, Jones, K(M)155398.

Notes: This species is characterised by large, pale yellowish-brown apothecia, ear-shaped, with agglutinated hairs (warts) on the exterior, pale hymenium, and small spores. A section of the apothecium reacts to KOH and becomes bright yellow, although in fungarium specimens only a dull yellow exudate has been observed. Fig. 1b indicates, as does the LSU phylogram by Olariaga *et al.*. (*op. cit.*), presence of three lineages (at least) in this species. Within the species clade, the British sequences cluster with other European collections but not placed in the same lineage as of the holotype. Nevertheless, the clade of the species is well supported as a whole (the ML bootstrap value 87) that the specimens within are all named *O. tuomikoskii*.

Species description: Apothecia gregarious, or clustered, earshaped, up to 6 cm tall, 'pale brown', Pale Ochraceous-Buff (XV15'f) in K(M)155378 and K(M)159720, drying Prout's Brown (XV15'm) or Buckthorn Brown (XV17'f). Hymenium pale whitish, Light Buff (XV17'f) in British collections, vary when drying, from Light Ochraceous-Buff (XV15'd), Light Buff (XV17'f), Ochraceous Tawny (XV15'i) to Tawny (XV13'). Ectal excipulum of textura angularis, cells globose when rehydrated, densely encrusted with yellowish brown crystals, surface markedly warty with agglutinated outgrowths, or villose. Subhymenium of textura intricata, hyaline or very pale yellow, not encrusted, cell walls yellow pigmented. Medullary excipulum of textura intricata, hyaline or very pale yellow, not encrusted, or with a very small amount of golden granules in places. Paraphyses slightly swollen at apices, mostly curved, hooked, often with a small notch, or a small protuberance, but some straight ones seen in K(M)137478. Ascospores 10.0–11.5 (–12.0) \times (5.5–) 6.0–6.5 (–7.0) μ m, 1.71 < Q < 1.85, av. 1.78 (n=54). Asci 170–175 \times 10–11 μ m. UV reactions when dry: outer surface Mummy Brown (XV17'm) under 254 nm, Buckthorn Brown (XV17'f) under 365 nm, hymenium Light Buff (XV17'f) or Warm Buff (XV17'd) under 254 nm, Light Buff under 365

Distribution outside Britain: Scandinavian countries, France, Germany, Spain, USA (Olariaga *et al..., op. cit.*), reported from Italy (Marini & Zanella, 2012), Switzerland (Christen & De Marchi, 2013), Russia (Svetasheva *et al...*, 2016) and China (Cao *et al...*, 1990).

4.-17 Unresolved taxa

Two *Otidea* collections at K from the 1930s could not be determined either morphologically or by molecular data. One of them, K(M)155462, with immature ascospores 17.0–20.0 \times 7.5–9.5 μm (in asci) and with dense yellow brown encrustation on ectal cells (Parslow & Spooner, 2013), may refer to *O. cantharella* but spores are too narrow, and was too immature for determination. Another, K(M)2943, has ascospores 15.0–17.0 \times (6.5–) 7.0–8.0 μm and yellow brown encrustation on the ectal cells.

5. Rejected names

5.-1 Scodellina Gray, Nat. Arr. Brit. Pl., 1: 668 (1821)

The English author S.F. Gray created a new genus, *Scodellina* (Gray, 1821), referring to MICHELI (1729) who, however, had used the word 'scodelline' only as an adjective (*op. cit.*: 206) and not as a generic name. Gray's concept of *Scodellina* was mixed, as his ten combinations included not only *Otidea* species (5), but also others which in modern terms should be variously referred to *Peziza*, *Aleuria*, *Ascobolus* and *Tarzetta*. Gray's first combination, *Scodellina leporina* (Pers.) Gray, had been considered the generic type (SEAVER, 1928; CLEMENTS & SHEAR, 1931). SEAVER (1928) considered that *Scodellina* should take precedence over *Otidea* (Pers.) Bonord. *Scodellina* is regarded as a *nomen confusum* which should not be used.

5.-2 Pseudotis (Boud.) Boud., Hist. classif. discomyc. Europe: 52 (1907).

Basionym: Otidea subgen. Pseudotis Boud., Bull. Soc. mycol. Fr., 1: 102 (1885).

BOUDIER (1885) created a new subgenus as a segregate from *Otidea*, to include species with more or less entire apothecia, and subsequently raised it to the rank of genus. It was considered a synonym of *Otidea* by Eckblad (1968) and Cannon *et al.*. (1985). We consider this a *nomen ambiguum* because of Boudier's mixed concept. In Britain, the combination *Pseudotis apophysata* (now *Otidea apophysata*) was adopted by Dennis (1968, 1978, 1981). The type species of *Pseudotis, P. abietina*, is considered a *nomen ambiguum* by Harmaja (2009), Carbone (2011), Parslow & Spooner (2013) and Olariaga *et al.*. (*op. cit.*).

5.-3 Not authentically British

The species, below, had previously been published as British (RAMSBOTTOM & BALFOUR-BROWNE, 1951; CANNON *et al..*, 1985; FRDBI online), however, no evidence for their presence here has been found in this study.

5.-3a Otidea cantharella (Fr.) Quél., Enchir. fung.: 275 (1886).

Basionym: Peziza cantharella Fr., Syst. mycol., 2(1): 48 (1822).

Misapplied by HARMAJA (1974) and subsequent British authors to *Otidea concinna* (see Notes of 4.-9). No true *O. cantharella* has been found in Britain.

5.-3b *Otidea integra* (Bres.) Harmaja, *Karstenia*, 26: 43 (1986). Basionym: *Otidea concinna* f. *integra* Bres., *Fungi Trident.*, 2: 70 (1898).

Mistakenly referred to as 'var. integra' by RAMSBOTTOM & BALFOUR-BROWNE (1951) and by CANNON et al.. (1985). Both entries were based on Carleton Rea's publication (Rea, 1916) of his 1915 collection from Eglinton Castle in Scotland, K(M)119617. In 1917, two additional collections were made at the same locality, K(M)119618 and 119619, originally deposited in Herb. BM(NH) and later transferred to K along with the other fungi collections. In 1967, John A. Nannfeldt examined K(M)119617 and K(M)119618 and determined them as O. phlebophora, accepted by R.W.G. Dennis. Subsequently, the name O. concinna var. integra was interpreted as a synonym of O. phlebophora (Cannon et al.., loc. cit.). All three Eglinton specimens are morphologically indistinguishable from O. phlebophora.

O. concinna f. integra, initially described by Bresadola (1898) and synonymised with O. phlebophora by Harmaja (1974), was later considered an independent species, O. integra Harmaja (Harmaja, 1986). No type specimen was designated by Bresadola, though the original protologue stated that this fungus had annually been found in Sopramonte near Trento. Olariaga et al.. (2015) examined a relevant Bresadola collection (S-F108342) and successfully extracted an ITS sequence from it which, in their ITS-LSU analysis (op. cit.: 174), clustered with O. minor. They concluded that O. integra was distinct, based on the ITS2 sequence of the Sopramonte specimen differing from the sequences of O. phlebophora, a conclusion supported by the current authors based on Fig. 1.

In the present study, no ITS sequence could be obtained from any of the Eglinton specimens, and no other British ITS clustered with S-F108342. Hence, *O. integra* remains to be proven British.

5.-3c *O. kauffmanii* Kanouse, *Mycologia*, 41: 673 (1949).

O. kauffmanii has previously been reported online as British (FRDBI) for two specimens, K(M)137477 and K(M)143475. However, these specimens have been re-determined in this study, as O. caeruleopruinosa and O. phlebophora respectively. OLARIAGA et al.. (2015) synonymised O. kauffmanii with O. rainierensis Kanouse based on the ITS-LSU tree, selecting the latter name by preference. No material matching O. rainierensis, i.e. O. kauffmanii, has been found in Britain.

5.-3d *O. papillata* Harmaja, *Karstenia*, 15: 31 (1976).

An online record of *O. papillata* collected 22 October 2012 from Northern Ireland (*ibid.*) is unsubstantiated with a voucher, so that at present this name should be excluded from the British species list. OLARIAGA *et al.*. (2015: 185) reported that *O. papillata* was only 'known from two Finnish collections', and that the name had been misapplied to similar species, *O. nannfeldtii* and *O. tuomikoskii*.

5.-4 Nomina dubia/ambigua

The names below had previously been published as British (RAMS-BOTTOM & BALFOUR-BROWNE, 1951; CANNON *et al.*., 1985), however, are rejected as a *nomen dubium* or a *nomen ambiguum* (OLARIAGA *et al.*., *op. cit.*, and in this study).

5.-4a *Otidea abietina* (Pers.) Fuckel, *Jahrb. Nassauischen Vereins Naturk.*, 23-24: 330 (1870).

Basionym: *Peziza abietina* Pers., *Neues Mag. Bot.*, 1: 113 (1794). Considered a *nomen ambiguum*.

5.-4b Otidea cochleata (L.) Fuckel, *Jahrb. Nassauischen Vereins Naturk.*, 23-24: 329 (1870).

Basionym: Peziza cochleata L., Sp. plant., 2: 1181 (1753).

Considered a nomen ambiguum (CARBONE, 2011; PARSLOW & SPOONER, 2013). CARBONE (op. cit.) selected a part of Bulliard's plate (1783-84, pl. 154, b, as *Peziza cochleata*) as the lectotype of *O. alutacea*. This selection should not automatically synonymise *Peziza cochleata* with *O. alutacea* (PARSLOW & SPOONER, 2015).

5.-4c Otidea felina (Pers.) Bres., *Fung. Trident.*, 2 (14): 103 (1900). Basionym: *Peziza felina* Pers., *Mycol. eur.*, 1: 223 (1822).

At present considered a *nomen ambiguum*. HARMAJA (2009), VAN VOOREN & CARBONE (2012) and PARSLOW & SPOONER (2013) all considered *O. felina* to be a synonym of *O. alutacea*. The last stated that, based on the morphology of British specimens, *O. felina* could refer either to *O. alutacea sensu stricto sensu* OLARIAGA *et al..*, or to their clade 3b. Two British collections previously named *O. felina*, K(M)155397 and K(M)155461, have been re-identified in this study as *O. tuomikoskii* and *O. onotica* respectively.

5.-4d *Otidea grandis* (Pers.) Rehm, *Bull. Soc. mycol. Fr.*, 9(2): 111 (1893).

Basionym: Peziza grandis Pers., Ann. Bot. (Usteri), 15: 27 (1795).

As suggested by HARMAJA (2009) and OLARIAGA *et al.*. (2015), we consider *O. grandis* a *nomen dubium*. This name has been most often applied to *O. bufonia* following REHM (1882, 1894), for which see also 4.-6. On one hand, HANSEN *et al.*. (2005) suggested that the original sense of *Peziza grandis* Pers. had been concordant with a *Peziza* species, and not with *Otidea*.

5.-5 To be placed elsewhere in modern taxonomy

Based on OLARIAGA *et al.*. (2015) and the present study, the species which had previously been published in Britain under *Otidea* (or *Pseudotis*, a synonym) combination (RAMSBOTTOM & BALFOUR-BROWNE, 1951, FRDBI online), but should belong elsewhere in modern taxonomy, are listed here.

5.-5a Otidea aurantia (Pers.) Massee, *Brit. Fung.-Fl.*, 4: 448 (1895). Basionym: *Peziza aurantia* Pers.

Is Aleuria aurantia (Pers.) Fuckel.

5.-5b *Otidea aurantia* var. *atromarginata* (W. Phillips & Plowr.) Massee, *Brit. Fung.-Fl.*, 4: 449 (1895).

Basionym: *Peziza aurantia* var. *atromarginata* W. Phillips & Plowr., *in* W. Phillips, *Man. Brit. Discomyc.*: 57 (1887).

Is a Melastiza sp.

5.-5c Otidea aurantia var. stipitata (W. Phillips) Massee, *Brit. Fung.-Fl.*, 4: 448 (1895).

Basionym: *Peziza aurantia* var. *stipitata* W. Phillips, *Man. Brit. Discomyc.*: 57 (1887).

A Sowerbyella sp. fide RAMSBOTTOM (1914), but uncertain due to lack of type material fide Spooner & Yao (1995).

5.-5d Otidea auricula (Schaeff.) Sacc., Syll. fung., 8: 95 (1889).

Basionym: *Peziza auricula* Schaeff., *Fung. bavar. palat. nasc.*, 2, pl. 156 (1763).

Is *Midotis lingua* Fr., formerly known as *Wynnella silvicola* (Sacc.) Nannf., i.e. *Helvella silvicola* (Sacc.) Harmaja (for synonymy see Hansen *et al..*, 2019). See also Parslow & Spooner (2009).

5.-5e *Otidea fibrillosa* Massee, *Brit. Fung.-Fl.*, 4: 449 (1895).

Is Pseudaleuria fibrillosa (Massee) Moravec.

5.-5f *Otidea luculenta* (Cooke) Massee, *Brit. Fungus-Fl.*, 4: 450 (1895).

Basionym: *Peziza luculenta* Cooke, *Mycographia*, Vol. 1. Discom. no. 3: 121, fig. 208 (1876).

Leucoloma luculentum (Cooke) Rehm. Possibly a species of Octospora Hedw.

5.-5g *Otidea luteonitens* (Berk. & Broome) Massee, *Brit. Fung.-Fl.*, 4: 449 (1895).

Basionym: *Peziza luteonitens* Berk. & Broome, *Ann. Mag. nat. Hist., Ser.* 2, 7: 180 (1851).

Holotype K(M)29982. Is Aleuria luteonitens (Berk. & Broome) Gillet.

5.-5h Otidea neglecta Massee, Grevillea, 22: 66 (1894).

Is Midotis lingua, as in 5.-5d (Parslow & Spooner, 2009).

5.-5i *Otidea radiculata* (Sow.) Bres., *Fung. Trident.*, 2: 72 (1892). Basionym: *Peziza radiculata* Sowerby, *Col. fig. Engl. Fung. Mushr.*, 1 (12), pl. 114 (1797).

Synonym: *Pseudotis radiculata* (Sow.) Boud., *Hist. Class. discom. Eur.*: 52 (1907).

Holotype K(M)30427. Is Sowerbyella radiculata (Sowerby) Nannf.

5.-5j *Otidea silvicola* Beck ex Sacc., *Syll. fung.*, 8: 97 (1889). Is *Midotis lingua*, as in 5.-5d. (Parslow & Spooner, 2009).

5.-5k *Otidea violacea* A.L. Sm. & Ramsb., *Trans. Br. mycol. Soc.*, 5 (2): 237 (1916).

The holotype, K(M)30407, is a Peziza (Parslow & Spooner, 2013).

5.-6 Disposition of 'Otidea austica (Pers.) Bonorden', a name created by human error

The name 'Otidea austica' appears at present on at least three British and two international websites. However, examination of Persoon's eleven and Bonorden's three major publications provided no evidence that they ever published this epithet nor the combination. (Persoon, 1796, 1797, 1799, 1801, 1803, 1804, 1805, 1808a, 1808b, 1818, 1822; Bonorden, 1851, 1864, 1870). The name is absent from other major 19th-century publications (e.g. Saccardo, 1889) which strongly suggests that it resulted from a typographic error.

The name appeared for the first time in 2003, in an unpublished report titled Database of Scottish records of Non-lichenised fungi, for Scottish National Heritage (SNH), authored by L.M. Davy. The report included two records of 'O. austica', both arising from the Nordic Mycological Congress excursions ('Dutch Jubilee Foray') based at Kindrogan Field Centre, Scotland, during 21-28 September 1983. One record was from Moulin and another from Blair Castle, both in East Perthshire. The records obtained from the excursions were later compiled into a species list and distributed to the participants. In early 2003, the author of the said report attempted to gather various Scottish fungi records, and by doing so received a typed list from the organiser of the 1983 Congress (Lynn Davy, pers. comm.), including two records which were then submitted to SNH. The specimens

and notes from the excursions had not been kept (Roy Watling, pers. comm.). It became clear that this name resulted from a typographic error made by a misreading of *Otidea onotica*.

Worse was to follow when, in 2004 'O. austica' was uploaded to FRDBI and to Index Fungorum online where it remained until 2006 when the first author requested of its removal. It reappeared briefly on Index Fungorum in 2008, and was then finally removed from the website. Harmaja (2009) confirmed that there was nothing in Persoon's Herbarium at L that referred to this epithet, supporting our theory. Recently, the name has reappeared on multiple websites, viz.: the Fungal Record Database of Britain and Ireland (FRDBI) where the name is marked 'doubtful'; the British National Biodiversity Network (NBN Atlas); the Natural History Museum ('Search for a UK species'); the Biological Library (BioLib); the Global Biodiversity Information Facility (GBIF), as if uncritically copied from one source to another. It is important that an erroneous name such as 'Otidea austica' should be deleted from all online resources so that it could no longer be duplicated.

Discussion and conclusion

Topology of the ITS phylogram

As explained above, the topology of the ITS phylogram obtained in this study (Fig. 1) shows some discrepancies with the multi-gene phylogram (HANSEN & OLARIAGA, 2015: 156). However, all clades of species are represented effectively, thus the current study is considered to have illustrated the species diversity of *Otidea* in Britain in full, except that the question of whether *O. cantharella* clade is truly missing from Britain or not remains to be answered.

This topology is similar to the LSU phylogram (OLARIAGA et al.., 2015: 173-174) in that O. flavidobrunneola appears as a sister clade to O. smithii, O. mirabilis and O. bufonia. Another question arises as to whether ITS sequences are as effective in interpreting intraspecific lineages (for example in O. bufonia and of O. onotica) as in species delimitation. To avoid this problem, deployment of multiple genes in phylogenetic analysis is recommended.

Geographical distribution of British species and taxa outside Britain

OLARIAGA *et al.*. (*op. cit.*) treated 22 named and two un-named species plus four taxa distributed in Europe, six species and two taxa endemic to North America, and four species and two taxa to Asia. One species, *O. integra*, was considered distinct based on DNA but not described in detail. Subsequently, two species have been newly described (CARBONE *et al..*, 2017; CARBONE *et al..*, 2019a), and one variety described (PARSLOW & SPOONER, 2015) raised to the rank of species (CARBONE *et al..*, 2019a). Resultantly, 26 species are now known from Europe.

All British species and taxa are present in Europe. In the Scandinavian countries, only *O. apophysata* and *O. adorniae* have yet to be recorded. Ten European species are still to be found in Britain, viz.: *O. cantharella, O. brunneoparva, O. propinquata, O. papillata, O. daliensis, O. mirabilis, O. borealis, O. integra, O. subformicarum* and *O. saliceticola*.

Bahram *et al.*. (2012) submitted one ITS sequence of *O. onotica* which originated from northern Iran. Barseghyan & Wasser (2013) stated that *O. alutacea* had been collected from two localities in Israel, one in the 1960s and another in 2007, both under *Quercus calliprinos*. However, the species description by the latter gave ascospore size as $10.8-11.8~(-12.7)\times5.9-6.9~\mu m$, smaller than typical *O. alutacea*. BILGRAMI *et al.*. (1979) reported *O. alutacea*, *O. bufonia* and *O. leporina* from India. We have not investigated any of these collections.

The species present both in Britain and in East Asia are: *O. alutacea* s. str., *O. leporina* and *O. bufonia* in China (OLARIAGA et al.., op. cit.). CAO et al.. (1990) suggested the Chinese presence of *O. onotica*, *O. concinna* and *O. tuomikoskii*, and MAO (2000), ZHUANG (2005) and LI

et al.. (2015) suggested that of *O. concinna*. Vouchers could not be located. One photograph of Japanese *O. onotica* by Y. Otani, published in IMAZEKI et al.. (1988: 574, right) agrees macroscopically with *O. onotica*. Otani's description of *O. onotica* (OTANI, 1989) agrees with that by OLARIAGA et al.. (2015) except in ascospore size, $10-12 \times 6-7$ μm, i.e. smaller than that in most European collections, $12-15 \times 6-7.5$ μm. However, at least two British *O. onotica* specimens do have smaller ascospores which fall within Otani's size range (see 4.-7), so that the Japanese description is tentatively accepted for *O. onotica*.

Of the 16 British species, those confirmed to be present also in North America are, based on the ITS, *Otidea onotica*, *O. leporina*, *O. nannfeldtii* and *O. tuomikoskii*. Hansen & Olariaga (2015: 159) suggested the presence of *O. bufonia* in North America, which is accepted here.

Within *O. alutacea*, clades 2 and 4 of OLARIAGA *et al.*. (*op. cit.*: 172) are at present known only in USA, and clade 6 of Xu *et al.*. (2018) only in China. Clade 7 was proposed by Xu *et al.*. (*loc. cit.*) based on a Swedish collection (ITS) which, in a subsequent phylogenetic study (CARBONE *et al..*, 2019), turned out clustered with the Chinese type of *O. kunmingensis* (ITS-LSU, ML BP 71%).

Summarising, all British *Otidea* species are considered of European origin. No evidence has been found to suggest direct introduction into Britain of species endemic to extra-Europe.

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Online resources

The Fungi Record Database of Britain and Ireland (FRDBI) http://www.frdbi.info

Taxonomic Literature II (TL-2)

http://www.sil.si.edu/DigitalCollections/tl-2/index.cfm

The Natural History Museum ('Search for a UK species')

https://www.nhm.ac.uk/our-science/data/uk-species/species

The British National Biodiversity Network (NBN Atlas) http://nbnatlas.org

Biological Library (BioLib)

https://www.biolib.cz/en/

The Global Biodiversity Information Facility (GBIF)

https://www.gbif.org/

New Zealand Fungi (NZFUNGI)

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