Persoonia 35, 2015: 166 – 229
www.ingentaconnect.com/content/nhn/pimj

RESEARCH ARTICLE

http://dx.doi.org/10.3767/003158515X688000

A monograph of *Otidea* (*Pyronemataceae, Pezizomycetes*)

I. Olariaga[1], N. Van Vooren[2], M. Carbone[3], K. Hansen[1]

Key words

Flavoscypha
ITS
ITS1 minisatellites
LSU
Otideopsis
resinous exudates

Abstract The easily recognised genus *Otidea* is subjected to numerous problems in species identification. A number of old names have undergone various interpretations, materials from different continents have not been compared and misidentifications occur commonly. In this context, *Otidea* is monographed, based on our multiple gene phylogenies assessing species boundaries and comparative morphological characters (see Hansen & Olariaga 2015). All names combined in or synonymised with *Otidea* are dealt with. Thirty-three species are treated, with full descriptions and colour illustrations provided for 25 of these. Five new species are described, viz. *O. borealis*, *O. brunneoparva*, *O. oregonensis*, *O. pseudoleporina* and *O. subformicarum*. *Otidea cantharella* var. *minor* and *O. onotica* var. *brevispora* are elevated to species rank. *Otideopsis kaushalii* is combined in the genus *Otidea.* A key to the species of *Otidea* is given. An LSU dataset containing 167 sequences (with 44 newly generated in this study) is analysed to place collections and determine whether the named *Otidea* sequences in GenBank were identified correctly. Fourty-nine new ITS sequences were generated in this study. The ITS region is too variable to align across *Otidea*, but had low intraspecific variation and it aided in species identifications. Thirty type collections were studied, and ITS and LSU sequences are provided for 12 of these. A neotype is designated for *O. cantharella* and epitypes for *O. concinna*, *O. leporina* and *O. onotica*, along with several lectotypifications. The apothecial colour and shape, and spore characters are important for species identification. We conclude that to distinguish closely related or morphologically similar species, a combination of additional features are needed, i.e. the shape of the paraphyses, ectal excipulum structure, types of ectal excipulum resinous exudates and their reactions in Melzer's reagent and KOH, tomentum and basal mycelium colours and exudates. The KOH reaction of excipular resinous exudates and basal mycelium are introduced as novel taxonomic characters.

Article info Received: 26 November 2013; Accepted: 1 February 2015; Published: 10 April 2015.

INTRODUCTION

Species of *Otidea* produce typically ear-shaped apothecia that are unique within *Pyronemataceae* (*Pezizomycetes*). The genus is monophyletic based on multilocus phylogenetic analyses from a few, but broadly sampled, *Otidea* species (Hansen et al. 2013). Despite being distinct at the generic level, the species identification and nomenclature of *Otidea* are highly controversial. A few recent typifications have been proposed (Carbone 2009, 2010a), but many names are still subjected to different interpretations. Several new species were described in the last decades from Europe (Harmaja 1976, 2009a) and Asia (Cao et al. 1990, Zhuang & Yang 2008), with detailed descriptions and updated identification keys. However, often no illustrations were presented and colour photographs have rarely been published when describing new species. Many names of European species currently used in North America and Asia are misapplied. Multilocus phylogenetic analyses have not been previously implemented to critically address species delimitation issues and material from different continents has not been compared. A worldwide critical revision of *Otidea* to clarify species limits is highly needed. The aims of this study were: i) to undertake a nomenclatural and taxonomic revision of *Otidea*, to clarify misinterpretations and to propose pertinent typifications to stabilise the use of names; and ii) to provide detailed species descriptions and colour photographs of both macro- and microscopic structures, and a key for identification. Our multilocus phylogenies and robust hypotheses of species limits, employing genealogical concordance phylogenetic species recognition (GCPSR; Taylor et al. 2000), which is the basis for the present work, are given in Hansen & Olariaga (2015). In the present study we present an LSU rDNA phylogeny to place a larger number of collections for which we have been unable to obtain multiple genes, including several sequences from GenBank, many of which we here re-identify.

Taxonomic history

The first valid publication of *Otidea* is by Bonorden (1851), based on *Peziza* (unranked) *Otidea* Pers., although it has sometimes been attributed to Fuckel (Kanouse 1949, Nannfeldt 1966, Liu & Zhuang 2006, Smith & Healy 2009). *Otidea* species were treated in a broad heterogeneous genus *Peziza* by early authors. Persoon (1822) defined *Peziza* (unranked) *Otidea* as producing auriculate apothecia with a split, sometimes elongated on one side, and included 10 species. Fries (1822) referred to this group as *Peziza* (unranked) *Cochleatae*, but he included also taxa with non-split apothecia. Bonorden (1851) elevated *Otidea* to generic rank with split apothecia as the key feature, but also referred to Fries' (1822) *Cochleatae*. He did not make any combinations or list any species. Fuckel (1870) refined the genus using microscopic details, namely uni- or biguttulate spores and filiform to subclaviform paraphyses, and included four species: *O. abietina*, *O. cochleata O. leporina* and *O. onotica*. Boudier (1885) notably contributed to disassemble the large genus *Peziza* into smaller and more natural genera. He placed in the genus *Otidea* species with entire or split apothecia, biguttulate spores and, importantly non-amyloid asci and curved paraphyses, which he was the first to introduce. He divided *Otidea* into two subgenera: *Otidea* with split

---

[1] Swedish Museum of Natural History, Department of Botany, P.O. Box 50007, SE-104 05 Stockholm, Sweden;
corresponding author e-mail: karen.hansen@nrm.se.
[2] 36 rue de la Garde, F-69005 Lyon, France.
[3] Via Don Luigi Sturzo 173 I-16148 Genova, Italy.

apothecia and *Pseudotis* with entire apothecia. Interestingly, Boudier erected the genus *Wynnella* (*Helvellaceae*) to accommodate *W. silvicola* (as *P. leporina* / *P. auricula*), a species with distinctly ear-shaped apothecia, but differing from *Otidea* in the uniguttulate spores and tough consistency. In Boudier's (1907) subsequent treatment, he elevated *Pseudotis* to genus rank and placed here species with entire apothecia, including *O. daliensis* (as *P. apophysata*) and *O. propinquata* (as *P. abietina*), both with biguttulate spores and hooked paraphyses. Saccardo listed *O. onotica* as an 'exemplar' species of *Peziza* subg. *Otidea* in his synopsis of the discomycete genera (1884; he listed in general only one species per genus / subgenus that appear to have been selected as typical for the genera) and it has since been accepted as the type species by most (Rifai 1968, Eckblad 1968, Korf 1972, Liu & Zhuang 2006, Parslow & Spooner 2013), Index Nominum Genericorum (Eckblad in Farr et al. 1979), NCU-3 (Greuter et al. 1993) and is prepared to be adopted on the List of Protected generic Names for fungi (Kirk et al. 2013). Clements & Shear (1931) listed *O. cochleata* as the type, but this name was not among the original species accepted by Persoon (1822) and has furthermore been considered an ambiguous name. Kanouse (1949) proposed *O. leporina* as the type species, but because of the confusions surrounding the identity of this species until now, it has been considered an inappropriate choice.

The genus *Scodellina* was described by Gray (1821) and involved species attributed today to *Otidea*, and also *Aleuria*, *Peziza* and *Tarzetta*. Seaver (1928) refined *Scodellina* to species with split to ear-shaped apothecia only and typified it with *Peziza leporina* (Seaver 1927), considering *Otidea* a later synonym. This was for a period followed by several American authors (e.g. Korf 1963, Kimbrough 1966). The typification by Seaver can however, be considered largely mechanical, taken as the first species listed by Gray, and be superseded under the ICN (Art. 10.5; McNeill et al. 2012). Also, even though Gray (1821) included several species with split apothecia, he did not mention this feature in the diagnosis of *Scodellina*, but emphasised "thallus … hemispherical, spreading" and coined the vernacular name "spread cup". Therefore Rifai (1968) designated *P. vesiculosa* Bull.: Fr. as the type species of *Scodellina*, consequently making it a later synonym of the genus *Peziza*. Eckblad (1968) came to the same conclusion.

Kanouse (1949) broadened the concept of *Otidea* and described in detail a number of North American species. She included species with split apothecia and straight paraphyses with swollen apices. She also included *Wynnella silvicola* (as *Otidea auricula*), with straight paraphyses and uniguttulate spores. Nannfeldt (1966) delimited *Otidea* to species with non-amyloid asci; smooth, uninucleate, biguttulate spores; a medullary excipulum of *textura intricata*; and an ectal excipulum with isodiametric cells, covered by short chains of barrel-shaped cells. Nannfeldt's concept more or less conforms to the genus *Otidea* as we recognise it today. He considered *Wynnella* so distant that it should be treated in a separate tribe of *Pezizaceae*. Korf (1963) reviewed the monotypic, sparassoid genus *Ascosparassis*, and subsequently (Korf 1973a) assigned *A. shimizuensis* to *Otidea*, based on the hooked paraphyses, small biguttulate spores and excipulum structure. Pfister (1979) however, considered *Ascosparassis* a distinct monotypic genus, based on "small asci and spores and peculiar growth habit", and combined the older name *Midotis heinricheri* in *Ascosparassis*. Later Pfister collected *A. heinricheri* in South America, in north coastal mountains of Venezuela (Pfister & Halling 1989), extending its Asian distribution (China, Indonesia and Japan), still considering the species separate from *Otidea*.

A new genus *Flavoscypha* was erected for two species of *Otidea*, *O. concinna* (as *Flavoscypha cantharella*) and *O. phlebophora*, with strong emphasis on the ectal excipulum of *textura prismatica* (vs *textura angularis* in *Otidea*) (Harmaja 1974). *Otidea* was further emended to include a species with ornamented spores, *O. unicisa*, otherwise 'fitting perfectly' *Otidea* (Harmaja 1986). *Otideopsis* was published with *Otideopsis yunnanensis* as the type species, distinguished from *Otidea* by having ornamented spores and paraphyses fused at the apices (Liu & Cao 1987). *Flavoscypha* and *Otideopsis* are now considered synonyms of *Otidea* based on molecular phylogenetic analyses (Liu & Zhuang 2006, Hansen & Olariaga 2015).

Recently the circumscription of *Otidea* was further broadened when the first hypogeous species, *O. subterranea*, was discovered using ITS and LSU sequences (Smith & Healy 2009). All the characters proposed so far as diagnostic for *Otidea* have exceptions across the genus. Nevertheless, *Otidea* can be recognised by the non-amyloid asci, in combination with at least two of these characters (except *O. subterranea*): a) biguttulate spores; b) hooked or bent paraphyses; c) medium-large, split apothecia; and d) a medullary excipulum of *textura intricata*, and an ectal excipulum of *textura angularis* or *textura prismatica*.

Systematic position and relationships

Nannfeldt (1937, 1938, 1966) suggested a close relationship between *Otidea* (incl. *Pseudotis*), *Tarzetta* (as *Pustularia*) and *Helvella* (*Pezizaceae*, tribe *Acetabuleae* sensu Nannfeldt), based on similarities in asci, paraphyses and anatomical structures of the apothecia, i.e. a medullary excipulum of dense *textura intricata*, ectal excipulum of almost isodiametric large cells, and an outermost layer of shorter or longer chains of cells, possible forming distinct clusters or warts (and in *Tarzetta* prolonged to cylindrical, hyaline, wavy hairs). Le Gal (1947) similarly placed *Otidea* in the tribe *Otideeae* in her *Aleuriaceae* (i.e. a family including taxa with both amyloid and non-amyloid asci), together with *Pseudotis* and *Tarzetta* (as *Pustularia*), but placed *Helvella* in *Helvellaceae*. Following the ideas of Nannfeldt (1966), Eckblad (1968) erected the family *Otideaceae* as a small taxon of closely related genera that produce larger apothecia, most of which typically lack bright orange to red colours, including in it *Tarzetta* (as *Pustulina*) and *Otidea*, but also *Ascosparassis*, *Geopyxis* and *Sowerbyella*. Eckblad considered *Helvella* (*Helvellaceae*) to be distant, but having a possible shared origin with members of *Otideaceae* (and *Morchellaceae* and *Rhizinaceae*), due to the structure of the excipulum, spores and asci, especially of *Tarzetta*. At the same time, he expanded the concept of *Pyronemataceae* (to 21 genera) to taxa mostly characterised by the presence of carotenoid pigments, stating the inability to satisfactorily subdivide the family on the basis of common characters. Korf (1972, 1973b) placed *Otidea* in the tribe *Otideeae* (in the subfamily *Otideoideae*) in an even more encompassing *Pyronemataceae* (49 genera), together with *Ascosparassis* and *Psilopezia*. He followed the ideas of Arpin (1969), in excluding taxa with carotenoids from the *Otideoideae*, instead including taxa with prominent hairs such as *Geopora*, *Humaria* and *Trichophaea*. *Otidea* has generally been included in a broadly circumscribed *Pyronemataceae* in recent treatments (Dissing 2000, Hansen & Pfister 2006, Perry et al. 2007, Hansen et al. 2013). Multigene phylogenetic analyses of *Pyronemataceae* do not support a close relationship between *Otidea* and *Geopyxis*, *Psilopezia*, *Sowerbyella* or *Tarzetta* (Hansen et al. 2013). Surprisingly, the cleistothecial *Warcupia* and the highly reduced (gymnohymenial) *Monascella* are suggested as the closest relatives of *Otidea*. *Otidea*, *Monascella* and *Warcupia* are strongly supported as a distinct sister group to the rest of the *Pyronemataceae* in a strict sense (Hansen et al. 2013).

MATERIALS AND METHODS

Material and morphological methods

This study is based on a total of 450 specimens. One hundred and forty two of these were collected and studied fresh during this project and are deposited in S and a few in TUR-A. Specimens were studied from the following herbaria: AH, ARAN, BIO, C, FH, H, HKAS, K, MCVE, MICH, MIN, OSC, PC, PRM, S, TUR and UPS (Thiers 2014), GMFN (gruppo AMB di Fara Novarese, Italy), SEST (Sociedad de Ciencias Naturales de Sestao, Spain), and from the private herbaria of G. Corriol, GC; C. Lavorato, CL; N. Van Vooren, NV; and M. Tabarés, MT. Thirty type collections were examined, along with other original material. Colour codes are based on Kornerup & Wanscher (1961). For *O. apophysata*, *O. borealis*, *O. daliensis*, *O. oregonensis*, *O. phlebophora*, *O. pseudoleporina*, *O. smithii* and *O. unicisa* colour codes for fresh material were taken from photographs. Apothecial sections, i.e. the thickness of the apothecia including the hymenium, was measured midway between the apothecial margin and base. Smell and taste are listed when recorded. Only discharged, mature spores were measured from living material. To obtain and ensure mature spores from dried material, a square of c. 3 mm^2 of an apothecium was revived in a drop of water on a slide, with the hymenium surface facing down and then removed after 1 hour. In this way mature spores deposited on top of the hymenium were recovered and measured. Spore measures exclude ornamentation. Spore statistics are based on measurements of 20 spores from each collection: L_m = mean length, W_m = mean width and $Q_m = L_m/W_m$. The number of populations that the statistics are based on is indicated by 'n'. Extreme values are given in parentheses. Hymenial elements were observed by teasing apart a small piece of hymenium with a needle. To observe the excipulum structure, sections of apothecia were made by hand prior to soaking the material in water. Basal mycelium was examined by mounting clumps of hyphae from the apothecial base (the tomentum) and from among the substrate particles. Only asci with mature spores were measured. All measurements were made in water: in living state whenever possible; only when not possible, measurements were made on rehydrated (over 2 hours in water) material. Melzer's reagent (MLZ) and 10 % KOH were used to observe the reaction of resinous exudates and other pigmentation. Cotton Blue in lactic acid was used to observe spore ornamentation. Microanatomical terminology follows Korf (1973b). The notation '!' indicates that type or other original material was examined by us.

If not otherwise indicated in the legends, the photographs presented in this paper were taken by K. Hansen and I. Olariaga.

DNA extraction, PCR amplification, sequencing and alignment

DNA was extracted from dried material, or from fresh material stored in 1 % SDS DNA extraction buffer. The extraction method follows Hansen et al. (1999), except dried material was ground in a Mini-Beadbeater™ (Biospec Products, Bartlesville, OK, USA) and fresh material using a plastic pestle, in eppendorf tubes. The primer combination ITS5-ITS4, and in a few instances ITS1–ITS4, ITS5–5.8S and ITS3–ITS4, were used to PCR amplify the ITS region, and LR0R–LR5 the LSU region. For DNA extracted from fresh material (stored in SDS extraction buffer), the ITS and LSU regions were amplified in a single piece using the primers ITS1–LR5. The ITS2 region for *O. integra* (possible original material from 1892) was successfully amplified in three pieces, in combination with newly designed primers for the *O. concinna* clade: ITS3 – *Conc*ITS2midR (5´-GCCTGTAAATTTTAAAGACGAA-3´); *Conc*ITS2midF (5´-CCAGGGTTGCTTTGGTA-3´) – *Conc*ITS4 intR (5´-CACTGGGTAATTGGAGGTTT-3´); *Conc*ITS2midF (5´-CCAGGGTTGCTTTGGTA-3´) – ITS4. PCR products were cleaned using ExoSAP-IT® (USB, Cleveland, OH, USA). The ITS was sequenced in both directions, using the primers ITS1 and ITS4 (and/or in a few instances ITS5, 5.8S and ITS3) and the LSU using LR0R and LR5. For *O. integra*, the same primers as used for PCR, were also used for sequencing. PCR and sequencing conditions follows Hansen & Olariaga (2015).

Sequences were edited and assembled using Sequencher v. 4.10 (Gene Codes Corporation Ann Arbor, Michigan, USA) and have been deposited in GenBank (Table 1). The sequences were aligned manually in Se-Al v. 2.0a11 Carbon (Rambaut 2002). An all taxa LSU dataset was prepared. *Monascella botryosa* and *Warcupia terrestris* were used as outgroup, based on a higher level phylogenetic study of *Pyronemataceae* (Hansen et al. 2013), which supports these as the closest sister group. To explore inter- and intraspecific variation of the new species *O. borealis*, *O. subformicarum* and their closest relatives, two smaller datasets were prepared using ITS and LSU rDNA sequences, based on a more species-inclusive, multi-gene phylogeny of *Otidea* (Hansen & Olariaga 2015). All three alignments are available from TreeBASE as accession no. S15887. The first dataset (the *O. borealis* dataset) contained *O. borealis* and related species in the *O. concinna* clade. The second dataset (the *O. formicarum* dataset) contained specimens of the *O. formicarum* clade. *Otidea caeruleopruinosa* and *O. nannfeldtii* were used as outgroup for each of these datasets. Nucleotide diversity (e.g. Nei 1987, equation 10.6), as the average number of nucleotide differences per sites between two ITS sequences, was calculated within *O. brunneoparva* and *O. subformicarum*. One insertion or deletion, despite the length, was calculated as only one basepair difference.

Phylogenetic analyses

Maximum Likelihood (ML) analyses of the all taxa LSU dataset were performed using the 'RAxML HPC2 on XSEDE' tool (Stamatakis 2006) via CIPRES Science Gateway (Miller et al. 2010), employing mixed models of evolution and starting from a random tree. For the two smaller *O. borealis* and *O. formicarum* datasets, ML analyses were conducted using RAxML v. 7.3.1 (Stamatakis 2006) on the Bioportal, University of Oslo (Kumar et al. 2009). A GTR-GAMMA model with four rate categories was assigned and all free model parameters were estimated by the program. For the ML bootstrap analyses (ML-BP) 1 000 rapid bootstrapping replicates from random starting trees were performed, followed by a subsequent ML search similarly using 1 000 replicates. As no strongly supported conflict was detected (ML-BP ≥ 75 %, PP ≥ 95 %), the ITS and LSU region were concatenated for the *O. borealis* and *O. formicarum* datasets. Each combined dataset was analysed using ML analyses under the same settings as specified above. Relationships were likewise constructed using Metropolis-coupled Markov Chain Monte Carlo (MCMCMC) and 'model-jumping' as implemented in MrBayes v. 3.2.1 (Ronquist et al. 2012). The substitution model was sampled across the GTR space by the MCMC analysis (Huelsenbeck et al. 2004). Four parallel searches, each with four chains, were run for ten and three million generations, respectively, for the all-inclusive LSU dataset and the *O. borealis* and *O. formicarum* datasets, initiated with random starting trees. The chains were sampled every 100 generations from the posterior distribution. The first 25 % of the trees sampled was discarded as the 'burn-in', and the remaining trees were used to calculate the posterior probabilities (PP) of the clades. For the combined ML and Bayesian analyses the ITS and LSU regions were specified as distinct partitions. ML bootstrap values ≥ 70 % and PP ≥ 95 % were considered to be significant.

Table 1 Collections used in the molecular phylogenetic analyses, with voucher information and GenBank accession numbers for ITS and LSU regions. Some GenBank sequences are re-identified by us and the names originally used in GenBank are listed after the taxon names ('as'). For type specimens (in **bold**) the original names are kept regardless of synonymy. Numbers in parentheses following the species names indicate multiple collections of a species. The GenBank accessions of sequences generated in this study are in **bold**.

Taxon	Voucher	Locality/year/collector	GenBank Accession no[4]	
			ITS	LSU
Monascella botryosa	**CBS 233.85**	Spain, 1985, J. Guarro	–	KC012688
Otidea alutacea (1)	KH.09.170 (S)	Sweden, 2009, K. Hansen & I. Olariaga	KM010059[1]	KC012691
O. alutacea (2)	KH.10.193 (S)	Sweden, 2010, K. Hansen, K. Gillen & I. Olariaga	KM010060[1]	KM823188[1]
O. alutacea (3)	KH.07.46 (S)	Denmark, 2007, H. Knudsen	**KM010061**	**KM823457**
O. alutacea (4)	JS.08.81 (S)	Sweden, 2008, J. Santos	KM010062[1]	KM823187[1]
O. alutacea (5)	OSC 56747	USA, 1996, E.T. Peterson	–	KM823189[1]
O. alutacea (6)	OSC 56770	USA, 1997, E.T. Peterson	–	AF072073
O. alutacea (7)	OSC 56798	USA, 1996, E.T. Peterson	–	AF086583
O. alutacea (8)	OSC 56777	USA, 1997, E.T. Peterson	–	AF086582
O. alutacea (9)	JS.08.43 (S)	Sweden, 2008, J. Santos	**KM010063**	**KM823458**
O. alutacea (10)	KH.09.135 (S)	Norway, 2009, V. Kučera & I. Kautmanova	KM010064[1]	KM823190[1]
O. alutacea (11)	KH.10.198 (S)	Sweden, 2010, K. Hansen, K. Gillen & I. Olariaga	**KM010065**	**KM823459**
O. alutacea (12)	KH.09.178 (S)	Sweden, 2009, K. Hansen & I. Olariaga	KM010066[1]	KM823191[1]
O. alutacea (13)	KS-94-192 (C)	Denmark, 1994, K. Hansen & S.K. Sandal	**KM010067**	**KM823460**
O. alutacea (14)	C-F-48045	Sweden, 1974, D. Paulsen & N. Tams	**KM010068**	**KM823461**
O. alutacea (15)	HMAS52742	China	–	DQ443438
O. alutacea (16)	HMAS57844	China	–	DQ443439
O. alutacea (17)	S-F257085	Italy, 2010, M. Carbone	KM010069[1]	KM823192[1]
O. alutacea (18)	Moorefun19 (OSC)	USA, 2010, J. Moore	KM010070[1]	KM823194[1]
O. alutacea (19)	OSC 56758	USA, 1996, E.T. Peterson	–	KM823193[1]
O. alutacea (20) as *O. umbrina*	OSC 56813	USA, 1997, E.T. Peterson	–	AF086584
O. alutacea (21) as *O. umbrina*	OSC 56782	USA, 2010, E.T. Peterson	–	AF086586
O. alutacea (22)	KH.09.133 (S)	Norway, 2009, K. Hansen & I. Olariaga	KM010071[1]	KM823185[1]
O. alutacea (23)	ARAN A3023204	Spain, 2009, J.I. López Amiano	KM010072[1]	KM823186[1]
O. alutacea (24)	GC 98092002	France, 1998, G. Corriol	**KM010073**	**KM823462**
O. alutacea (25)	HMAS83560	China, 2003, W.Y. Zhuang & Y. Nong	–	DQ443442
O. alutacea (26)	HMAS83563	China, 2003, W.Y. Zhuang & Y. Nong	–	DQ443440
O. alutacea (27)	KS-94-111 (C)	Denmark, 1994, K. Hansen & S.K. Sandal	**KM010074**	**KM823463**
O. alutacea (28)	HMAS83559	China, 2003, W.Y. Zhuang & Y. Nong	–	DQ443441
O. alutacea (29)	S-F257084	Italy, 2010, M. Carbone	**KM010075**	**KM823464**
O. alutacea (30)	KH.13.50 (S)	Sweden, 2013, K. Hansen & X. Wang	**KM010076**	**KM823465**
O. angusta	**H6010804**	Finland, 1965, H. Harmaja	KF717574[1]	KM823195[1]
O. apophysata	S-F257062, dupl. private herb. Kasparek s.n.	Germany, 1999, F. Kasparek	KM010077[1]	KM823196[1]
O. borealis	**S-F242694**	Finland, 2010, M. Carbone	KM010023[1]	KM823197[1]
O. brevispora as *O. onotica* var. *brevispora*	**HKAS 43003**	China, 2003, Z.L. Yang	–	DQ443450
O. brunneoparva (1)	KH.09.82 (S)	Sweden, 2009, K. Hansen & I. Olariaga	KM010029[1]	KM823198[1]
O. brunneoparva (2)	S-F249386 (Ex-H6017193)	Finland, 1978, H. Harmaja	**KM010024**	**KM823466**
O. brunneoparva (3)	S-F257086, dupl. TUR–A 198579	Finland, 2009, M. Carbone	KM010025[1]	KM823199[1]
O. brunneoparva (4)	JS.08.66 (S)	Sweden, 2008, J. Santos	**KM010028**	**KM823467**
***O. brunneoparva* (5)**	**KH.08.107 (S)**	Sweden, 2008, K. Hansen	KM010026[1]	KM823200[1]
O. brunneoparva (6)	TUR-A 198582	Finland, 2011, M. Lahti	**KM010027**	**KM823468**
O. bufonia (1)	KH.09.172 (S)	Sweden, 2009, K. Hansen & I. Olariaga	JN942764	JN941097
O. bufonia (2)	JS.08.55 (S)	Sweden, 2008, J. Santos	**KM010078**	**KM823469**
O. bufonia (3)	KH.07.37 (S)	Denmark, 2007, K. Hansen	JN942767	JN941098
O. bufonia (4)	KH.09.248 (S)	Spain, 2009, J.L. Teres & P.M. Pasaban	JN942766	JN941084
O. bufonia (5)	KH.09.249 (S)	France, 2009, J.L. Teres	KM010079[1]	KM823201[1]
O. bufonia (6)	NV 2009.11.01 (S)	France, 2009, G. Moyne	JN942765	JN941085
O. bufonia (7)	C-F-94240	Denmark, 2011, M. Sasa	**KP119674**	–
O. caeruleopruinosa (1)	**H6010805**	Finland, 1978, H. Harmaja	KF717575[1]	KM823202[1]
O. caeruleopruinosa (2)	MT 10082601 (SCM, dupl. S)	Spain, 2010, M. Tabarés & S. Santamaría	KM010030[1]	KM823203[1]
O. caeruleopruinosa (3)	KH.13.48 (S)	Sweden, 2013, I.-L. Walter	**KM010081**	**KM823470**
O. cantharella (1)	JS.08.18 (S)	Sweden, 2008, J. Santos	**KM010082**	**KM823471**
O. cantharella (2)	JS.08.47 (S)	Sweden, 2008, J. Santos	**KM010083**	**KM823472**
***O. cantharella* (3)**	**KH.09.125 (S)**	Sweden, 2009, K. Hansen & I. Olariaga	KM010084[1]	KM823205[1]
O. cantharella (4)	NV 2008.09.16 (dupl. S)	France, 2008, J. Cavet	KM010085[1]	KM823204[1]
O. concinna (1)	JS.08.59 (S)	Sweden, 2008, B. Wasstorp	**KM010031**	**KM823473**
***O. concinna* (2)**	**KH.09.183 (S)**	Sweden, 2009, K. Hansen & I. Olariaga	KM010032[1]	JN941089
O. concinna (3)	KH.09.250 (S)	Spain, 2009, F. Prieto & A. González	JN942775	JN941095
O. crassa	**HMAS583571**	China, 2003, W.Y. Zhuang & Y. Nong	–	DQ443444
O. daliensis (1)	**HMAS57688**	China, 1988, S. Wang & W.Y. Zhuang	–	DQ443445
O. daliensis (2)	SEST-06081702	Spain, 2003, J.L. Pérez Butrón	KM010086[1]	KM823206[1]
O. flavidobrunneola (1)	**H6010806**	Finland, 1978, H. Harmaja	KF717576[1]	KM823209[1]
O. flavidobrunneola (2)	H6010830	Finland, 1987, P. Askola	KM010087[1]	KM823208[1]
O. flavidobrunneola (3)	KH.09.153 (S)	Norway, 2009, K. Hansen & I. Olariaga	KM010088[1]	KM823207[1]
O. formicarum (1)	H6003350	Finland, 2005, U. Salo & P. Salo	**KM010036**	**KM823474**
O. formicarum (2)	JS.08.63 (S)	Sweden, 2008, J. Santos	KM010035[1]	KM823212[1]
***O. formicarum* (3)**	**H6003549**	Finland, 1970, L. Fagerström	KF717577[1]	KM823211[1]
O. formicarum (4)	S-F244372 (dupl. O)	Norway, 2009, J. Lorås	KM010034[1]	KM823210[1]
O. formicarum (5)	KH.11.104 (S)	Sweden, 2011, J.C. Zamora & I. Olariaga	**KM010033**	**KM823475**
O. fusconigra	GMFN 2293	Italy, 2003, G. Jamoni	**KM010037**	**KM823476**
O. integra	S-F108342	Italy, 1892, G. Bresadola	**KP006504**	–
O. kauffmanii (1)	AH21147 (MICH)	USA, 1917, A.H. Smith & R.J. Porter	AF072095	–

Table 1 (cont.)

Taxon	Voucher	Locality / year / collector	GenBank Accession no[4]	
			ITS	LSU
O. kauffmanii (2)	**MICH14409**	USA, 1915, C.H. Kauffman	**KF717579**	–
O. kaushalii	T. Læssøe 6236 (C, dupl. BORH)	Malaysia, 1999, T. Læssøe	KM010119[1]	AF335111
O. lactea	**HMAS61359 (ex-MHSU 1803)**	China, 1987, J. Z. Cao	–	DQ443447
O. leporina (1)	HMAS83579	China, 2003, W.Y. Zhuang & Y. Nong	–	DQ443448
O. leporina (2)	HMAS83568	China, 2003, W.Y. Zhuang & Y. Nong	–	DQ443449
O. leporina (3) as *O. smithii*	–	–	–	AF086573[2]
O. leporina (4)	OSC 56824	USA, 1997, E.T. Peterson	–	KM823216[1]
O. leporina (5)	OSC 56784	USA, 1997, E.T. Peterson	–	KM823215[1]
O. leporina (6) as *O.* sp.	HMAS583570	China, 2003, W.Y. Zhuang & Y. Nong	–	DQ443443
O. leporina (7)	JS.08.46 (S)	Sweden, 2008, J. Santos	**KM010089**	**KM823477**
O. leporina (8)	**KH.09.93 (S)**	Sweden, 2009, K. Hansen & I. Olariaga	KM010090[1]	KM823213[1]
O. leporina (9)	JS.08.92 (S)	Sweden, 2008, J. Santos	**KM010091**	**KM823478**
O. leporina (10)	NV 2008.09.28 (dupl. S)	France, 2008, N. Van Vooren	KM010092[1]	KM823214[1]
O. microspora	AH30502 (MICH)	USA, 1948, A.H. Smith	AF072094	–
O. minor (1)	H6003841	Finland, 2006, U. Salo & P. Salo	**KM010040**	**KM823479**
O. minor (2)	KH.10.311 (S)	Sweden, 2010, K. Hansen, K. Gillen & I. Olariaga	KM010042[1]	KM823218[1]
O. minor (3)	H6008618	Finland, 1992, R. Saarenoksa	KM010039[1]	KM823219[1]
O. minor (4)	TL-Vorsø-0754 (C)	Denmark, 1982, T. Læssøe	**KM010043**	**KM823480**
O. minor (5)	CL 950914-01 (dupl. S)	Italy, 1995, C. Lavorato	KM010044[1]	KM823220[1]
O. minor (6)	KH.98.84 (C)	Denmark, 1998, K. Hansen	KM010041[1]	KM823217[1]
O. minor (7)	C-F-83445	Denmark, 2007, T. Læssøe	**KM010038**	**KM823481**
O. mirabilis (1)	KH.09.188 (S)	Sweden, 2009, E. Bohus-Jensen, K. Hansen & I. Olariaga	JN942770	JN941086
O. mirabilis (2)	KH.10.285 (S)	Sweden, 2010, K. Hansen, K. Gillen & I. Olariaga	KM010094[1]	KM823221[1]
O. mirabilis (3) as *O. umbrina*	KH.01.09 (C)	Denmark, 2001, C. Lange	JN942769	AY500540
O. mirabilis (4)	S-F257083	Finland, 2010, M. Carbone	**KM010095**	**KM823482**
O. mirabilis (5)	NV 2008.09.14 (dupl. S)	France, 2008, J. Cavet	JN942768	JN941094
O. mirabilis (6)	**S-F256929**	Italy, 1999, D. Bolognini	**KF717580**	**KM823483**
O. myosotis	**H6003548**	Finland, 1970, L. Fagerström	KF717578[1]	KM823222[1]
O. nannfeldtii (1)	CL 091116-17 (S)	Italy, 2009, C. Lavorato	**KM010096**	**KM823484**
O. nannfeldtii (2)	S-F257096	Italy, 2009, B. De Ruvo	**KM010097**	**KM823485**
O. nannfeldtii (3)	CL 091207-01 (S)	Italy, 2009, C. Lavorato	**KM010098**	**KM823486**
O. nannfeldtii (4) (= *O. lohjaënsis* nom. prov. Harmaja)	S-F249387 (Ex-H6017194)	Finland, 1978, H. Harmaja	KM010093[1]	KM823225[1]
O. nannfeldtii (5)	JS.08.103 (S)	Sweden, 2008, J. Santos	KM010045[1]	KM823224[1]
O. nannfeldtii (6)	NV 2008.10.01 (dupl. S)	France, 2008, N. Van Vooren	KM010099[1]	KM823227[1]
O. nannfeldtii (7)	**H6002902**	Finland, 1972, C.-A. Haeggström	KF717581[1]	KM823228[1]
O. nannfeldtii (8)	rh101310 (OSC)	USA, 2010, R. Helliwell	KM010100[1]	KM823226[1]
O. nannfeldtii (9)	KH.10.302 (S)	Sweden, 2010, K. Hansen, K. Gillen & I. Olariaga	KM010101[1]	KM823223[1]
O. onotica (1)	OSC 56801	USA, 1997, E.T. Peterson	AF072067	AF086578
O. onotica (2)	OSC 56734	USA, 1996, E.T. Peterson	AF072066	AF086577
O. onotica (3)	OSC 56759	USA, 1996, E.T. Peterson	–	JN941088
O. onotica (4)	C-F-89691	Denmark, 2008, H. Knudsen	JN942773	JN941090
O. onotica (5)	JS.08.48 (S)	Sweden, 2008, J. Santos	**KM010102**	**KM823487**
O. onotica (6)	**KH.10.284 (S)**	Sweden, 2010, K. Hansen, K. Gillen & I. Olariaga	KP006505[1]	KM823229[1]
O. onotica (7)	KH.09.132 (S)	Norway, 2009, K. Hansen & I. Olariaga	**KM010103**	KC012692
O. onotica (8)	KH.09.136 (S)	Norway, 2009, K. Hansen & I. Olariaga	JN942772	JN941096
O. onotica (9)	MCVE 23277	Italy, 2008, M. Carbone	**KM010104**	**KM823488**
O. onotica (10)	KH.98.107 (C)	Denmark, 1998, K. Hansen, T. Læssøe & C. Lange	–	AF335121
O. oregonensis (1)	rh139 (S)	USA, 2010, R. Helliwell	**KM010046**	**KM823489**
O. oregonensis (2)	**Moorefun 58** (OSC, S)	USA, 2010, J. Moore	KM010048[1]	KM823231[1]
O. oregonensis (3)	Moorefun 31 (S)	USA, 2010, J. Moore	KM010047[1]	KM823230[1]
O. oregonensis (4) as *O. rainierensis*	OSC 56829	USA, 1997, M. Castellano	AF072087	AF086597
O. oregonensis (5) as *O. rainierensis*	NSW6354 (OSC)	USA, 1990, D. McKay	AF072088	AF086598
O. oregonensis (6) as *O. rainierensis*	OSC 56745	USA, 1996, J. Trappe	AF072089	KM823232[1]
O. oregonensis (7)	EGS2179 (MICH)	USA, 1948, E.G. Simmons	AF072088	–
O. papillata (1)	**H6003547**	Finland, 1971, H. Harmaja	KF717582[1]	KM823234[1]
O. papillata (2)	TUR 102134	Finland, 1990, T. Lindholm	KM010105[1]	KM823233[1]
O. papillata f. _pallidefurfuracea_	**NV 2007.09.27 (S)**	France, 2007, N. Van Vooren	KF717584[1]	KM823235[1]
O. phlebophora (1)	JV06-385 (C)	Denmark, 2006, L. & J. Vesterholt	KM010049[1]	KM823236[1]
O. phlebophora (2)	S-F108338	Sweden, 1949, G. Haglund & R. Rydberg	**KM010050**	**KM823490**
O. phlebophora (3)	K(M)33068	UK	EU784392	–
O. platyspora (1)	KH.09.163 (S)	Sweden, 2009, K. Hansen & I. Olariaga	KM010106[1]	KM823238[1]
O. platyspora (2)	HK0846 (S)	Sweden, 2008, H. Kauffman	**KM010107**	**KM823491**
O. platyspora (3)	JV06-656 (C-F-75309)	Denmark, 2006, J. Vesterholt	KM010108[1]	KM823237[1]
O. propinquata (1)	KH.09.99 (S)	Sweden, 2009, K. Hansen & I. Olariaga	KM010109[1]	KM823239[1]
O. propinquata (2)	JS.08.67 (S)	Sweden, 2008, J. Santos	**KM010110**	**KM823492**
O. propinquata (3)	NV 2008.09.15 (dupl. S)	France, 2008, J. Cavet	KM010111[1]	KM823240[1]
O. pseudoleporina (1) as *O. concinna*	NSW7574 (OSC)	USA, N. S. Weber	AF072083	AF086593
O. pseudoleporina (2) as *O. concinna*	OSC 56749	USA, 1996, E.T. Peterson	AF072082	AF086592
O. pseudoleporina (3) as *O. concinna*	OSC 56760	USA, 1996, E.T. Peterson	AF072081	KM823244[1]
O. pseudoleporina (4)	**rh101910 (OSC)**	USA, 2010, R. Helliwell	KM010112[1]	KM823243[1]
O. pseudoleporina (5)	Moorefun 14 (S)	USA, 2010, J. Moore	KM010113[1]	KM823242[1]
O. pseudoleporina (6)	OSC 56809	USA, 1997, J. Spatafora	AF072080	KM823241[1]
O. rainierensis	**A.H. Smith 30553 (MICH)**	USA, 1948, A.H. Smith	KF717583[1]	KM823245[1]
O. sinensis	HMAS61360	China	–	DQ443451
O. smithii (1)	OSC 56799	USA, 1997, E.T. Peterson	AF072063	JN941087
O. smithii (2)	ecv3345 (S)	USA, 2005, E. Vellinga	JN942771	JN941093

Table 1 (cont.)

Taxon	Voucher	Locality / year / collector	GenBank Accession no[4]	
			ITS	LSU
O. smithii (3)	OSC 56753	USA, 1996, E.T. Peterson	AF072062	AF086574
O. smithii (4)	OSC 56811	USA, 1997, E.T. Peterson	AF072060	AF086572
***O. subformicarum* (1)**	**S-F242696**	Spain, 2012, J. Herranz & J.C. Campos	**KM010054**	**KM823495**
O. subformicarum (2)	S-F256979	Spain, 2008, J. Fernández Vicente et al.	**KM010051**	**KM823494**
O. subformicarum (3)	CL 050928-30, dupl. S-F256978	Italy, 2005, C. Lavorato	KM010052[1]	KM823247[1]
O. subformicarum (4)	Private herb. CMP 1179, RM 1095, dupl. S-F256980	Spain, 2009, C. M. Pérez del Amo & R. Gil	KM010053[1]	KM823246[1]
O. aff. *subformicarum* (1)	FH301035	Mexico, 2007, M. Hernández	KM010055[1]	KM823249[1]
O. aff. *subformicarum* (2)	FH301036	Mexico, 2007, M.E. Smith	KM010056[1]	KM823248[1]
O. subterranea (1)	RH97 (FH)	USA, 1997, R. Healy	FJ404766	FJ404766
O. subterranea (2)	**RH69** (FH)	USA, 1997, R. Healy	FJ404767	FJ404767
O. tuomikoskii (1)	JS.08.68 (S)	Sweden, 2008, J. Santos	**KM010114**	**KM823496**
O. tuomikoskii (2)	MK200065 (S)	Sweden, 2000, M. Karström	**KM010115**	**KM823497**
O. tuomikoskii (3)	**H6002901**	Finland, 1972, R. Tuomikoski	KF717585[1]	KM823250[1]
O. tuomikoskii (4)	JS.08.100 (S)	Sweden, 2008, J. Santos	**KM010116**	**KM823498**
O. tuomikoskii (5)	NV 2008.09.08 (S)	France, 2008, N. Van Vooren	JN942777	JN941091
O. tuomikoskii (6)	KH.09.130 (S)	Norway, 2009, K. Hansen & I. Olariaga	JN942776	JN941092
O. tuomikoskii (7)	KH.11.77 (S)	Sweden, 2011, M. Prieto & I. Olariaga	**KM010117**	**KM823499**
O. tuomikoskii (8) as *O. leporina*	–	–	–	AF086588[3]
O. tuomikoskii (9)	OSC 56756	USA, 1996, E.T. Peterson	AF072084	AF086594
O. tuomikoskii (10)	OSC 56826	USA, 1996, M. Madsen & R. Davis	AF072086	AF086596
O. tuomikoskii (11)	OSC 56761	USA, 1996, E.T. Peterson	AF072085	KM823251[1]
O. unicisa (1)	KH.06.06 (FH)	USA, 2006, L. Millman	–	KC012693
O. unicisa (2) as *O. grandis*	HMAS51684	USA, Burdsall	–	DQ443446
O. unicisa (3) as *O. grandis*	ZW Geo65-Clark (S)	USA, 2003, Z. Wang	**KM010118**	AY789369
O. yunnanensis	HMAS 82166	China, 2003, Z.L. Yang	–	DQ443452
O. sp. ‘a’ (1)	MK0942 (S)	Sweden, 2009, M. Karström	**KM010057**	**KM823500**
O. sp. ‘a’ (2)	MK1081 (S)	Sweden, 2010, M. Karström	**KM010058**	**KM823501**
O. sp. ‘b’	KH.09.79 (S)	Sweden, 2009, K. Hansen & I. Olariaga	KM010120[1]	KM823252[1]
Warcupia terrestris	CBS 891.69	Canada, 1966, J.W. Paden	–	DQ220467

[1] Sequences from Hansen & Olariaga (2015).

[2] The voucher specimen for AF086573 is mistakenly given as OSC 56823 in GenBank. This voucher (OSC 56823) is *O. smithii* based on morphological re-examination and the ITS sequence (AF072061) deposited by the same authors. The LSU sequence AF086573 is *O. leporina* (Fig. 1).

[3] The voucher specimen for AF086588 is mistakenly given as OSC 56825 in GenBank. This voucher (OSC 56825) is *O. leporina* based on morphological re-examination and the ITS sequence (AF072078) deposited by the same authors. The LSU sequence AF086588 is *O. tuomikoskii* (Fig. 1).

[4] ITS: Internal transcribed spacers (ITS1 and ITS2) and the 5.8S gene of the nrDNA; LSU: 28S large subunit of the nrRNA gene.

RESULTS

Alignment and ITS minisatellites

Fourty-nine ITS and 44 LSU sequences were newly generated in this study (Table 1). In total 146 ITS sequences were utilised, including 34 obtained from GenBank and 63 from Hansen & Olariaga (2015). The ITS sequences were too variable to align across all of *Otidea*, due to a highly polymorphic part in ITS1 and large length variability (insertions and deletions), and therefore were not included in phylogenetic analyses of the entire genus. The ITS sequences were aligned among closely related species or species groups, and used as an aid to verify identifications. The ITS region was especially useful in cases were the protein-coding genes (RPB1, RPB2 and EF1) failed to amplify, due to poor quality DNA from old or poorly treated material. ITS sequences of the type specimens of *O. mirabilis* and *O. kauffmanii* that could not be amplified for the multiple genes are provided here. The all taxa LSU alignment consisted of 167 LSU sequences, including 57 from GenBank and 68 from Hansen & Olariaga (2015) (Table 1) and 956 bp including inserted gaps, of which 263 bp were parsimony informative characters.

The *O. borealis* dataset consisted of 31 taxa, represented by 24 complete ITS-LSU and six ITS sequences, and 1 555 bp including inserted gaps (ITS 614 bp; LSU 941 bp), of which 216 were parsimony informative characters. The *O. formicarum* dataset consisted of 14 sequences and 2 531 bp (ITS 1 695 bp; LSU 836 bp). Part of the ITS1 (805 bp) in the *O. formicarum* dataset was omitted from the analyses, due to a long insertion and tandem repeats in *O. subformicarum* and the two Mexican specimens, and the combined dataset thus included 1 726 bp, of which 145 were parsimony informative characters. The insertion was composed of four tandem repeats (minisatellites) in the four *O. subformicarum* sequences (212 bp in total), and in one of them (S-F256979) the repeat was present a fifth time (275 bp in total). In the Mexican FH301036 the insertion was extremely long (715 bp in total), of variable to random repeats. The tandem repeats were 43 or 63 nucleotides. They were composed of three parts (A-B-C) of 30, 20 and 13 nucleotides, respectively, which were duplicates of the preceding part of the ITS1 sequence. In the first two repeats the B part was missing, whereas in the third-fifth all parts were present. The C part was 100 % identical in all specimens and repeats; the A part was mostly identical, but showed 3.3–6.7 % variation in one repeat; and the B part showed 5–15 % variation in the repeats. To ascertain the correctness of the long insertion in the Mexican specimens, the ITS sequence of FH301036 was amplified and sequenced twice, using different sets of primers (in one piece using ITS1-ITS4 and in two pieces using ITS5-5.8S / ITS3-ITS4). The two sequences were found to be identical. Unfortunately, we were not able to sequence the complete insertion of FH301035 and the ITS1 was only sequenced in one direction; both the part of the insertion recovered and the ITS1 were highly different from FH301036.

All taxa LSU phylogeny

The ML analysis of the all taxa LSU dataset resulted in a single best ML tree of -lnL = 6511.68. Bayesian analyses reached an average standard deviation of split frequencies of 0.004 after 10 M generations. A majority rule consensus tree was constructed from the 300 000 trees sampled from the four runs, each consisting of 75 000 trees sampled from the station-

Fig. 1 Bayesian inference 50 % majority rule consensus phylogram of *Otidea* from LSU sequence data. Maximum Likelihood bootstrap values (ML-BP) ≥ 70 % and Bayesian posterior probabilities (PP) ≥ 95 % are shown above and below the branches, respectively. Thickened branches received support by both ML-BP ≥ 70 % and PP ≥ 95 %. Type collections are highlighted in **bold**. Country of origin for each collection is given using ISO country codes. Names of species recognised are indicated by the vertical bars.

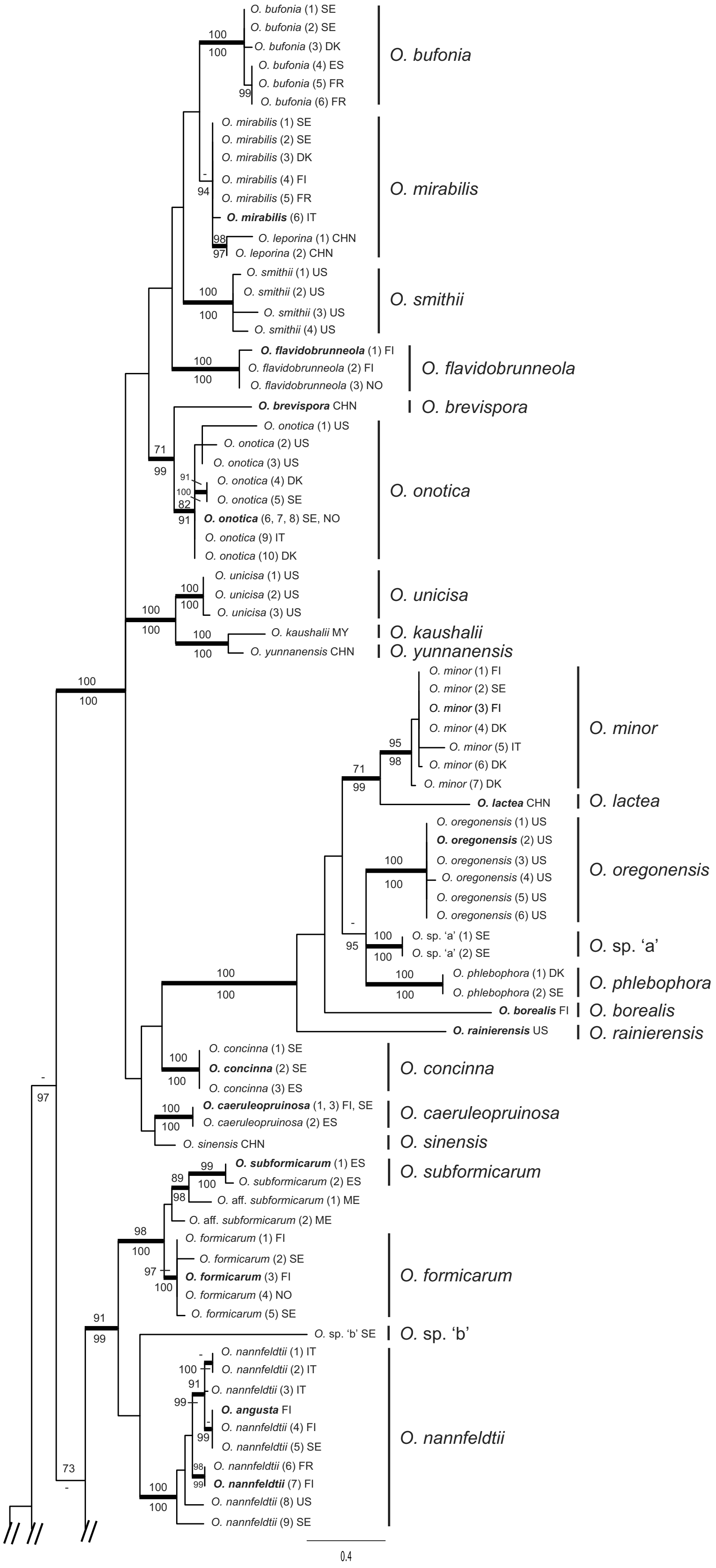
O. bufonia (1) SE
O. bufonia (2) SE
100
100
O. bufonia (3) DK
O. bufonia (4) ES
O. bufonia (5) FR
99
O. bufonia (6) FR
O. bufonia
O. mirabilis (1) SE
O. mirabilis (2) SE
O. mirabilis (3) DK
-
94
O. mirabilis (4) FI
O. mirabilis (5) FR
O. mirabilis (6) IT
O. mirabilis
98
97
O. leporina (1) CHN
O. leporina (2) CHN
O. smithii (1) US
100
O. smithii (2) US
100
O. smithii (3) US
O. smithii (4) US
O. smithii
100
100
O. flavidobrunneola (1) FI
O. flavidobrunneola (2) FI
O. flavidobrunneola (3) NO
O. flavidobrunneola
O. brevispora CHN
O. brevispora
O. onotica (1) US
O. onotica (2) US
71
99
O. onotica (3) US
91
100
82
91
O. onotica (4) DK
O. onotica (5) SE
O. onotica (6, 7, 8) SE, NO
O. onotica (9) IT
O. onotica (10) DK
O. onotica
O. unicisa (1) US
100
100
O. unicisa (2) US
100
100
O. unicisa (3) US
O. unicisa
100
100
O. kaushalii MY
O. yunnanensis CHN
O. kaushalii
O. yunnanensis
100
100
O. minor (1) FI
O. minor (2) SE
O. minor (3) FI
O. minor (4) DK
95
98
O. minor (5) IT
O. minor (6) DK
71
99
O. minor (7) DK
O. minor
O. lactea CHN
O. lactea
O. oregonensis (1) US
O. oregonensis (2) US
100
100
O. oregonensis (3) US
O. oregonensis (4) US
O. oregonensis (5) US
O. oregonensis (6) US
O. oregonensis
-
95
100
100
O. sp. 'a' (1) SE
O. sp. 'a' (2) SE
O. sp. 'a'
100
100
O. phlebophora (1) DK
O. phlebophora (2) SE
O. phlebophora
100
100
O. borealis FI
O. borealis
O. rainierensis US
O. rainierensis
100
100
O. concinna (1) SE
O. concinna (2) SE
O. concinna (3) ES
O. concinna
-
97
100
100
O. caeruleopruinosa (1, 3) FI, SE
O. caeruleopruinosa (2) ES
O. caeruleopruinosa
O. sinensis CHN
O. sinensis
99
100
O. subformicarum (1) ES
O. subformicarum (2) ES
O. subformicarum
89
98
O. aff. subformicarum (1) ME
O. aff. subformicarum (2) ME
98
100
O. formicarum (1) FI
O. formicarum (2) SE
97
100
O. formicarum (3) FI
O. formicarum (4) NO
O. formicarum (5) SE
O. formicarum
91
99
O. sp. 'b' SE
O. sp. 'b'
-
100
O. nannfeldtii (1) IT
O. nannfeldtii (2) IT
91
99
O. nannfeldtii (3) IT
O. angusta FI
-
99
O. nannfeldtii (4) FI
O. nannfeldtii (5) SE
98
99
O. nannfeldtii (6) FR
O. nannfeldtii (7) FI
73
-
100
100
O. nannfeldtii (8) US
O. nannfeldtii (9) SE
O. nannfeldtii
0.4

Fig. 1 (cont.)

ary tree distribution (the first 25 % discarded as the burn-in) (Fig. 1). The ML and Bayesian tree topologies were congruent and recovered the same moderate to strongly supported clades (Fig. 1). The terminal clades that constitute species we recognise (Hansen & Olariaga 2015) have moderate to strong support in both analyses, except for *O. leporina* and *O. mirabilis*. A few synonymies inferred from sequences of type collections from which we were not able to obtain the protein-coding genes, and clear misidentifications of sequences deposited in GenBank are evidenced by the LSU phylogeny (see Table 1). Based on LSU sequences from GenBank: the holotype of *O. crassa* is nested within the *O. leporina* clade (= *O. leporina* and *O. pseudoleporina*); *O. lactea* is suggested to be a sister lineage to *O. minor; O. sinensis* is resolved as a sister species to *O. caeruleopruinosa*, but without support; *O. yunnanensis* forms a monophyletic group with *O. kaushalii* and *O. unicisa;* and the type of *O. onotica* var. *brevispora* (= *O. brevispora*) is supported as a sister lineage to *O. onotica.* The holotype of *O. mirabilis* is nested among other collections of *O. mirabilis* and the LSU sequence differs only in 1 bp from sequences of collections from Scandinavia and France.

The O. formicarum and O. concinna clades in separate ITS-LSU phylogenies

The ML analysis of the *O. formicarum* dataset recovered a single tree of -lnL = 3579.93 (Fig. 2). Bayesian analyses reached an average standard deviation of split frequencies of 0.003 after 3 M generations. A majority rule consensus tree was constructed from the 90 004 trees sampled from the four runs, each consisting of 22 501 trees sampled from the stationary tree distribution (the first 25 % discarded as the burn-in). The four collections of *O. subformicarum* from Spain and Italy form a distinct, strongly supported monophyletic group (ML-BP and PP 100 %). Likewise, the five collections of *O. formicarum* from Fennoscandia, and the two collections of *O.* aff. *subformicarum* from Mexico, each form separate, strongly supported clades (ML-BP and PP 100 %; ML-BP 84 %, PP 100 %, respectively). Phylogenetic analyses of the combined ITS-LSU dataset fail however, to resolve relationships among these three clades with any certainty.

The combined ML analysis of the *O. borealis* dataset resulted in a single best ML tree of -lnL = 4230.82 (Fig. 3). Bayesian analyses reached an average standard deviation of split frequencies of 0.005 after 3 M generations. A majority rule consensus tree was constructed, as for the *O. formicarum* dataset (above). The supported topology (PP ≥ 95 %) did not differ from the supported topology recovered by ML analysis. The placement of the single *O. borealis* collection is unresolved, but the ITS-LSU phylogeny confirms it is genetically divergent from its sister species (Fig. 3). Other species with a yellow outer surface of the apothecia, *O. concinna*, *O. minor*, *O. oregonensis* and *O. phlebophora*, are each strongly supported as monophyletic (ML 97–99 %, PP 100 %). An exception is *O. minor* (5) from Italy that is resolved as a sister lineage to the rest of the *O. minor* collections and *O. integra* without support. The ITS and LSU sequences of *O. minor* (5) differ by 16 and 5 bp, respectively, from the rest of the sequences of *O. minor*, which are 100 % identical, except for the ITS sequence of *O. minor* (7) that differs in 1 bp. *Otidea integra* is represented only by the ITS2 region (281 bp). The holotype of *O. rainierensis* is forming a

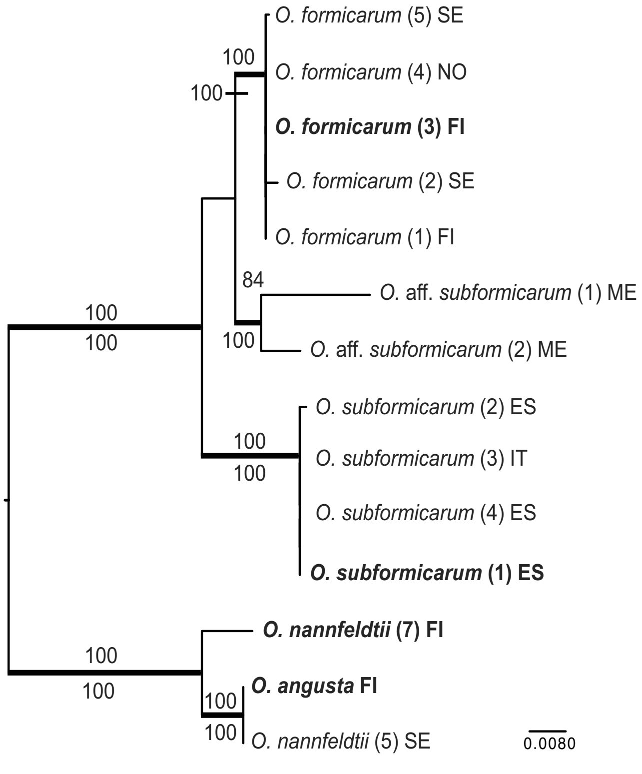

Fig. 2 The single best tree resulting from the Maximum Likelihood analysis of the ITS-LSU regions of the *O. formicarum* clade. ML bootstrap values (ML-BP) are shown above nodes and Bayesian posterior probabilities (PP) below nodes. Thickened branches are nodes with high support (ML-BP ≥ 75; PP ≥ 95). Type collections are in **bold**.

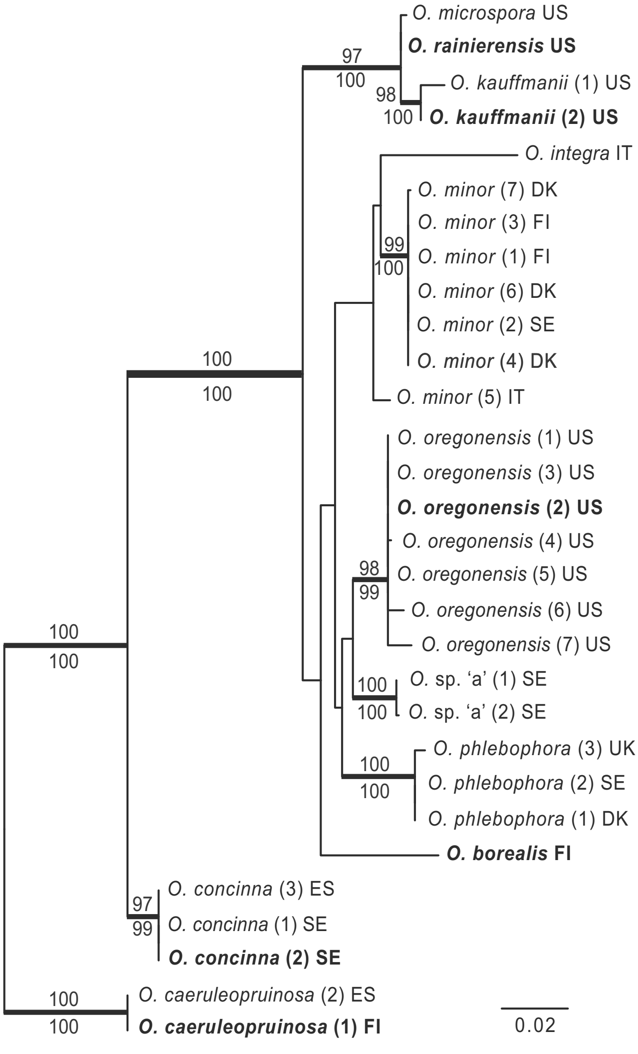

Fig. 3 The single best tree resulting from the Maximum Likelihood analysis of the ITS-LSU regions of *O. borealis* and closely allied species. ML bootstrap values (ML-BP) are shown above nodes and Bayesian posterior probabilities (PP) below nodes. Thickened branches are nodes with high support (ML-BP ≥ 75 %; PP ≥ 95 %). Type collections are in **bold**.

strongly supported clade with the holotype of *O. kauffmanii* and a paratype of *O. microspora* (ML 97 %, PP 100 %). The *O. kauffmanii* and *O. microspora* types are only represented by ITS and are therefore not included in any of our previous analyses. We conclude *O. kauffmanii* is a synonym of *O. rainierensis* and *O. microspora* a doubtful name (see further under Taxonomy). *Otidea concinna* is strongly supported as a sister group to the rest of the ingroup, but otherwise the relationships among the species are without support.

The phylogenetic results, and the ITS sequence similarity and divergence (for species identification), will be further discussed where applicable in the descriptive notes below.

Morphological characters for species delimitation

All *Otidea* species recognised by concordance of our four genes phylogenies (Hansen & Olariaga 2015) can be recognised by a combination of morphological characters. We evaluated the characters in the context of the phylogeny and discovered several new characters. The apothecial shape, colours, and spore characters (size, shape, ornamentation) are important for species identification, but to distinguish closely related species (or otherwise morphologically similar species) additional characters are needed. These are the shape of the paraphyses, ectal excipulum structure, type of exudates on the medullary excipulum hyphae, resinous exudates on the outer surface of the ectal excipulum and on the mycelium at the base of the apothecia, and their possible reactions in MLZ and KOH (see further in Hansen & Olariaga 2015). Below we provide details on the resinous exudates, and their reactions in KOH and MLZ, because they largely have been overlooked.

Excipular resinous exudates and reactions in MLZ and KOH

A resinous exudate is here used for a substance that is released from the cells and in many species is vulnerable to common mountants, but not water (following Huhtinen 1990). In *Otidea* the exudates are concentrated in the excipulum cells, and on the tomentum and mycelium at the base of the apothecia. The resinous exudates are deposited on the outside of the cell or hyphal walls. Harmaja (2009a) introduced the reaction of coloured resinous exudates on the outermost cells of the ectal excipulum in MLZ as a taxonomic character. Our study revealed in addition, different reaction patterns of exudates on the medullary excipulum cells and on the mycelium at the base of the apothecia (including the tomentum), extending out among the soil particles, which turned out to be diagnostic for some species (see under Mycelium at the base of the apothecia). In the medullary excipulum, most frequently scattered, golden brown, resinous exudates are present at septa, e.g. in *O. alutacea*, *O. leporina*, *O. nannfeldtii* (Fig. 4a). *Otidea bufonia* has unique exudates, wrapping some hyphae and appearing striate (referred to as 'fingerprint-like' by Korf & Zhuang (1991)), sometimes forming big crystal-like aggregates (Fig. 4b, c). In contrast, the sibling species, *O. mirabilis*, has only sometimes biflabellate crystal-like exudates in the medullary excipulum (Fig. 4d). *Otidea papillata* also possesses unique brown exudates, embedding some hyphae of the medullary excipulum and sometimes appearing rod-like.

Small, resinous drops or amorphous matter are present in variable amounts on the outer surface of the apothecia of nearly all *Otidea* species. In most species they are abundant and

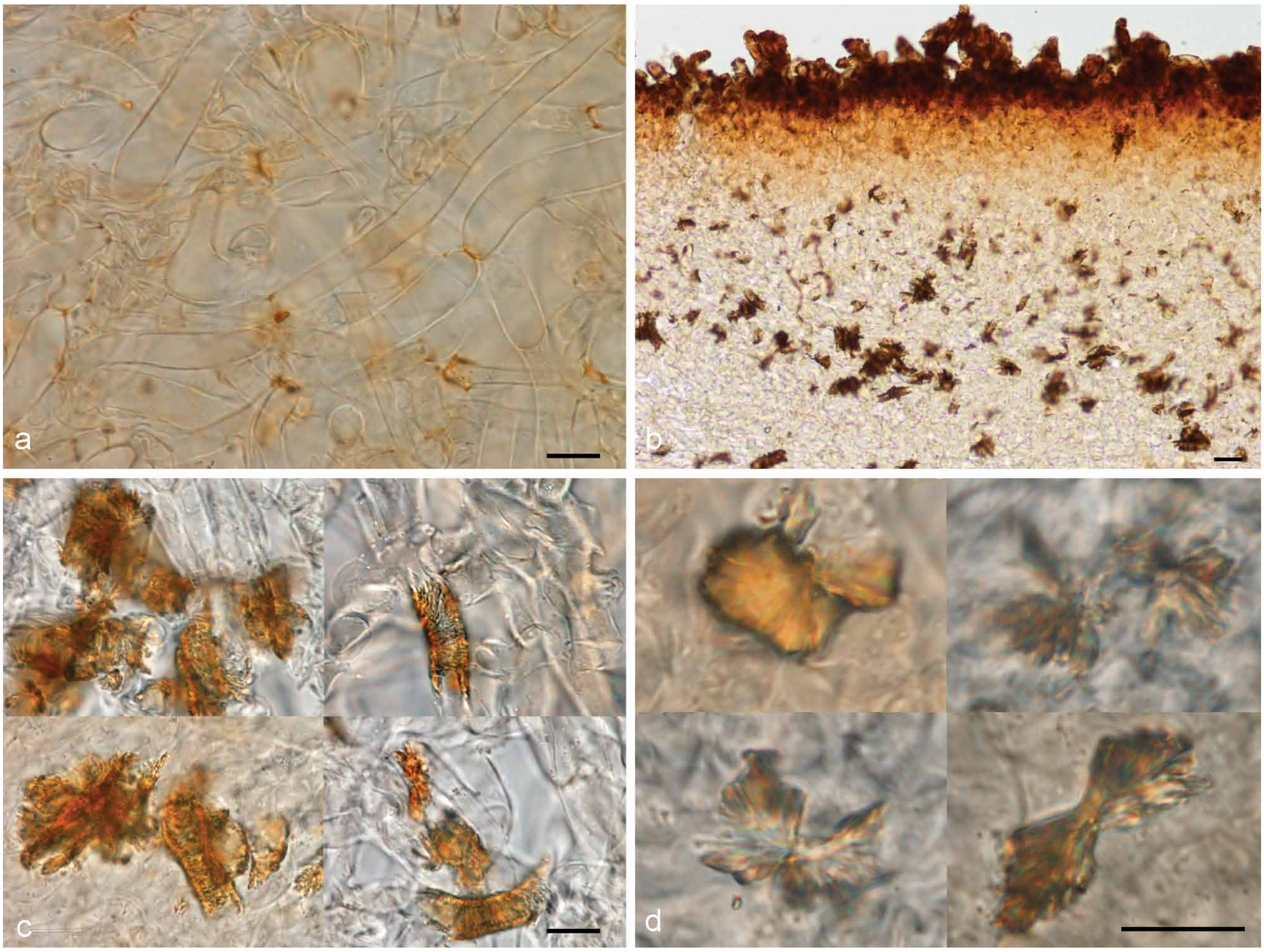

Fig. 4 Medullary excipulum resinous exudates in *Otidea*. a. Hyphae with golden brown resinous exudates at septa in *O. leporina* (KH.11.02), in water*; b, c. brown crystal-like exudates in *O. bufonia* (KH.07.37) in water†: b. overview; c. close-up of hyphae wrapped in striate exudates; d. close-up of biflabellate crystal-like exudates in *O. mirabilis* (GMFN 1951, holotype), in water† — Scale bars = 10 µm; * = fresh material; † = dried material.

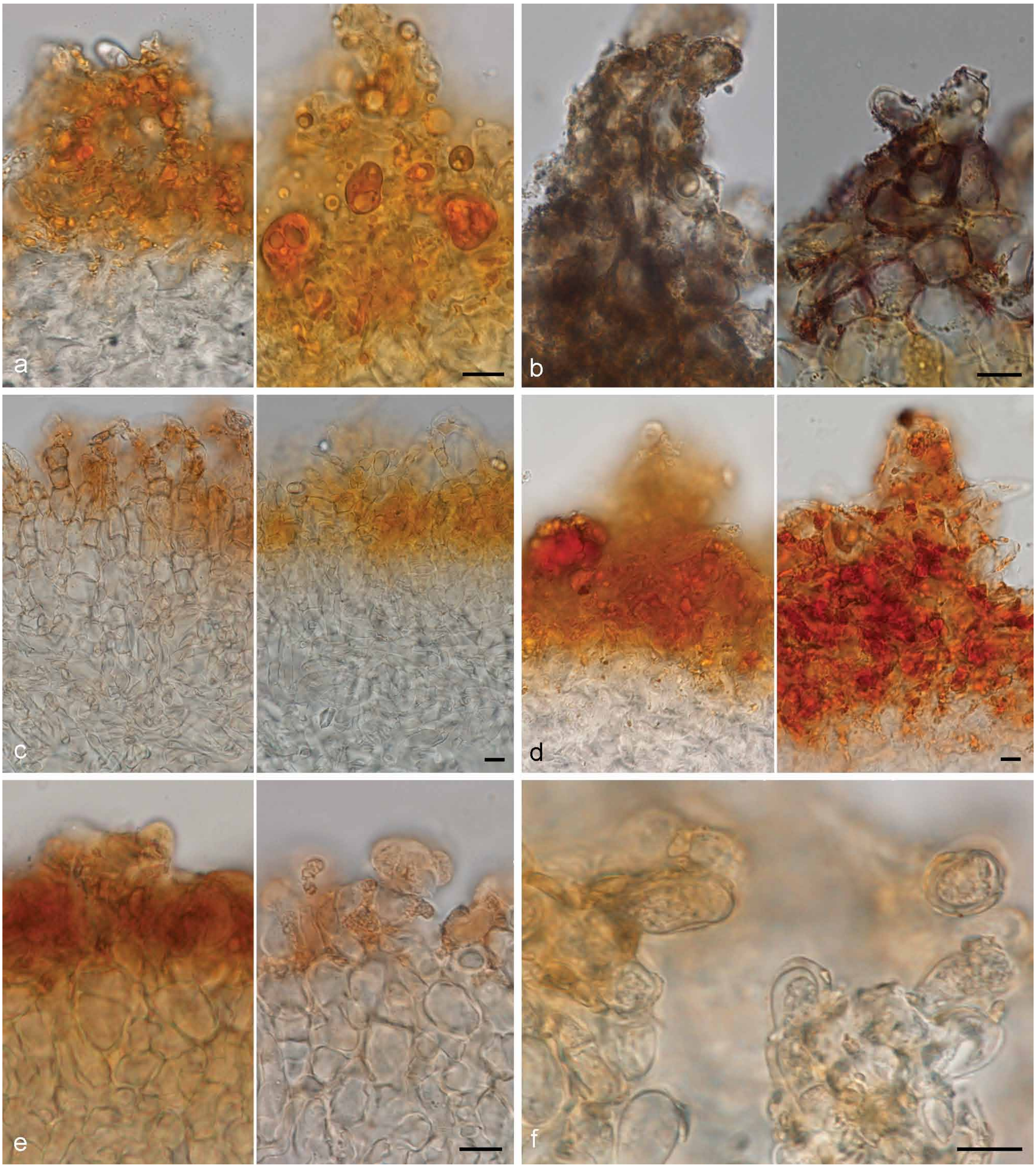

Fig. 5 Reactions of resinous exudates on the outermost ectal excipulum cells in *Otidea*. a. *O. nannfeldtii*† (H6010804, holotype of *O. angusta*), in water (left) and converting into amber drops in Melzer's reagent (right); b. *O. bufonia** (KH.09.171), in water (left) and converting into reddish particles in Melzer's reagent (right); c. *O. borealis*† (S-F242694, holotype), in water (left) and turning bright yellow in KOH (right); d. *O. nannfeldtii*† (H6010804), in water (left) and turning reddish brown in KOH (right); e. *O. pseudoleporina*† (rh101910, holotype), in water (left) and converting into reddish grey drops in KOH (right); f. ectal excipulum cells showing a gelatinous sheath in *O. formicarum** (KH.11.104). — Scale bars = 10 µm; * = fresh material; † = dried material.

easy to observe in water, but scarce and difficult to detect in a few (*O. alutacea*, *O. formicarum*). One species, *O. kaushalii*, has a unique type of exudate, i.e. crystal-like, oblate spheroid, striate bodies, with a constricted centre. The possible reaction of the exudates in MLZ and KOH is useful to separate certain species or groups. Using these characters requires experience. The reaction appears to vary depending on the amount of exudate and the concentration of MLZ. As Harmaja (2009a), we observed two types of reactions in MLZ: i) Resinous exudates dissolve and coalesce into spheroid drops, 'amber drops', that contain hyaline bubbles (Fig. 5a). The 'amber drops' are overlooked if the ectal excipulum is directly mounted in MLZ, since the exudates coalesce instantly and the drops can be washed away. The reaction is best observed if MLZ is added to a water mount. This reaction is present in many species. ii) Resinous exudates partly convert into small reddish particles (Fig. 5b). The reaction is often subtle and visible only in certain parts of a mount. This reaction is typical in *O. bufonia*, *O. mirabilis* and *O. smithii*. In some species the exudates do not react in MLZ or they simply dissolve.

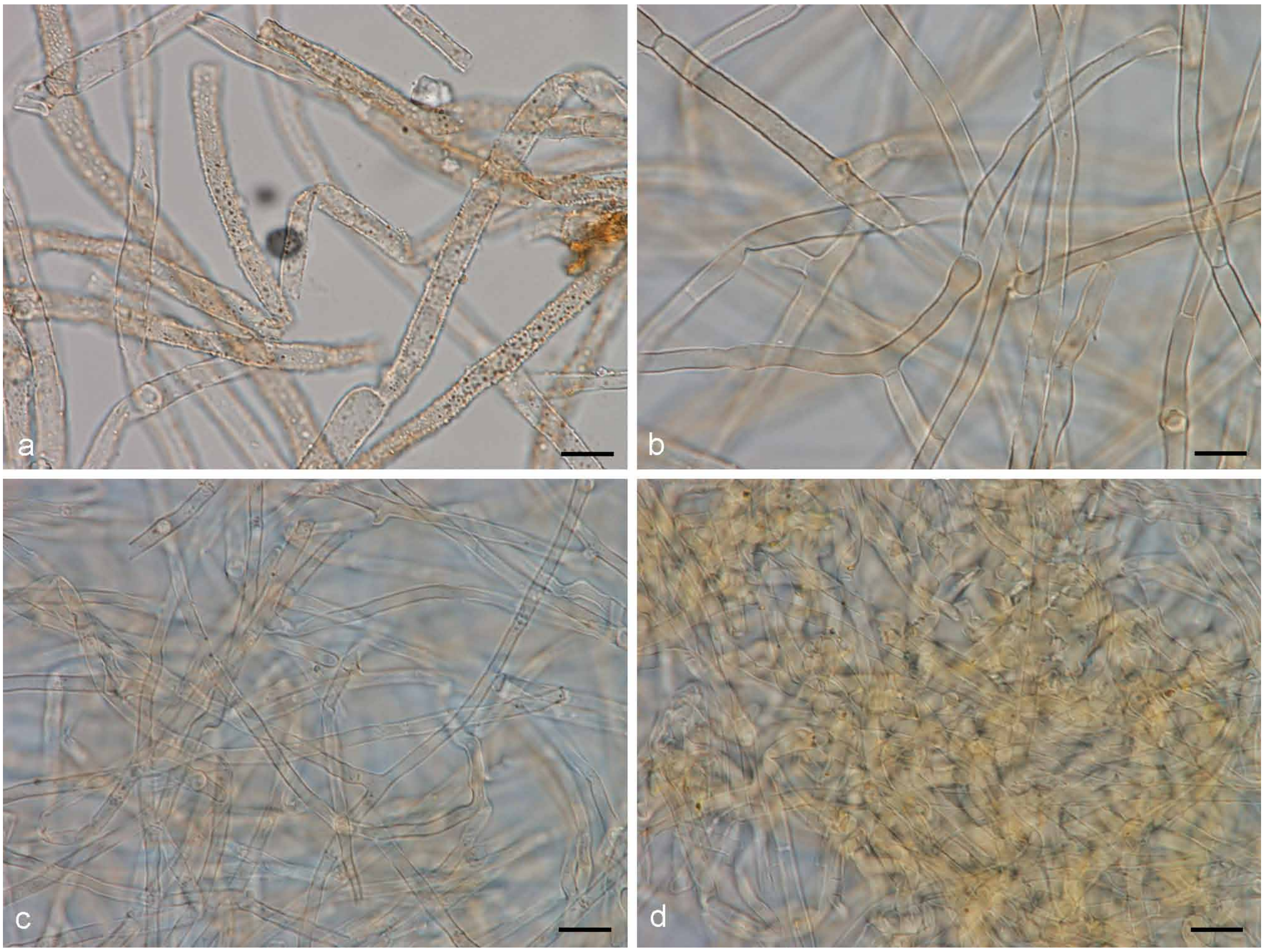

Fig. 6 Mycelium at the base of the apothecia and extending out in the substrate in *Otidea*†. a, b. *O. flavidobrunneola* (H6010806, holotype): a. resinous exudates on the hyphal walls in water; b. dissolved in Melzer's reagent; c, d. *O. borealis* (S-F242694, holotype): c. pale yellow in water; d. turning bright yellow in KOH. — Scale bars = 10 µm; † = all dried material.

In this study we detected three discriminative reactions of resinous exudates in 10 % KOH, which we propose as a novel taxonomic character: i) In water the resinous exudates range from yellow to dark reddish yellow (Fig. 5c, left) and in KOH these dissolve completely ± exuding a yellow pigment, or partly with the rest turning distinctly brighter yellow (Fig. 5c, right). This reaction occurs in *O. concinna* and closely related species, viz. *O. borealis*, *O. caeruleopruinosa*, *O. flavidobrunneola*, *O. kaushalii*, *O. minor* and *O. oregonensis*, and slightly less strikingly in *O. unicisa*. ii) The resinous exudates are yellow-brown in water (Fig. 5d, left) and turn reddish brown in KOH (Fig. 5d, right). This reaction has been observed in *O. nannfeldtii* and *O. propinquata*. iii) The resinous exudates, yellow brown in water (Fig. 5e, left), partly dissolve in KOH, and partly coalesce into heterogeneous, pale reddish grey drops, with bubbles inside (Fig. 5e, right). These drops are similar to the 'amber drops' observed in MLZ in many species, except for the pale red colour. This reaction has been observed in *O. leporina* and *O. pseudoleporina*. A number of species have the outermost cells of the ectal excipulum sometimes covered with a thin gelatinous sheath (Fig. 5f).

Mycelium at the base of the apothecia

All *Otidea* species studied showed a conspicuous tomentum covering the base of the apothecia and spreading out in the substrate. In the microscopic descriptions we refer to both as the basal mycelium. The hyphae are septate, straight and frequently branch and anastomose. No rhizomorphs have been observed, although slender hyphal threads are sometimes formed. Resinous exudates are often present on the surface, especially on the mycelia extending out in the substrate, and can appear like hyphal ornamentation.

Harmaja (2009a) proposed the colour of the basal tomentum as a taxonomic character, but microscopic features of the basal mycelium have been largely overlooked and have not been included in species descriptions. Two types of characters are useful for species identification: i) Resinous exudates occurring on the hyphal walls (Fig. 6a). These can be inconspicuous or nearly absent in some species, such as in *O. alutacea* s.l., in which only a few refractive drops or minute hyaline exudates are sometimes present. Resinous exudates are also scarce in some species of the *O. concinna* clade. Many other species show hyphae densely covered with resinous exudates, such as *O. formicarum*, *O. propinquata* and *O. tuomikoskii*. The shape of the exudates is variable, i.e. rod-shaped, hemispherical, conical or bipyramidal. They dissolve and completely disappear in MLZ (Fig. 6b). Sometimes doubts can arise about the nature of the differently shaped exudates, but the facts that they detach from the hyphal wall when the mount is squashed and dissolve in MLZ, show these are not true ornamentation, i.e. not part of the hyphal wall. ii) The hyphal wall turns yellow in KOH (Fig. 6d; see Fig. 6c in water). We have observed this reaction clearly in *O. borealis* and *O. onotica*. It can be observed in isolated hyphae, but is more conspicuous when a mass of hyphae is observed together. It can also be observed macroscopically.

TAXONOMY

Otidea (Pers.) Bonord., Handb. Mykol.: 205. 1851

≡ *Peziza* (unranked) *Otidea* Pers., Mycol. Eur. 1: 220. 1822.
≡ *Peziza* (unranked) *Cochleatae* Fr., Syst. Mycol. 2: 46. 1822: Fr. loc. cit.
Type species. *Otidea onotica* (Pers. : Fr.) Fuckel, indicated by Saccardo, Bot. Centralbl. 18: 215. 1884 (‘*P. onotica* Pers.’).
= *Flavoscypha* Harmaja, Karstenia 14: 107. 1974.
Type species. *Peziza phlebophora* Berk. & Broome.
= *Otideopsis* B. Liu & J.Z. Cao, Shanxi Univ. J., Nat. Sci. Ed. 4: 70. 1987.
Type species. *Otideopsis yunnanensis* B. Liu & J.Z. Cao.

Apothecia small to large, 3–75 mm high, 4–80 mm wide, often in fascicles or caespitose, epigeous, cup- to ear-shaped and split to the base on one side, less often entire, stipitate or not; or hypogeous and enclosed. *Hymenium* white, yellow, ochre, brown, almost black, often with pink stains. *Receptacle surface* concolorous or with similar colours as hymenium, sometimes with purplish, greenish or bluish tones, with conical to broadly conical warts or pustules, less often smooth or furfuraceous, concolorous or darker than the background. Base of the apothecium tomentose, mycelium white, ochre, yellow, orange or brown, extending out in the substrate, base ribbed-veined in a few species. *Spores* uniseriate, ellipsoid, oblong or fusoid, typically with 2 guttules, sometimes with a few smaller granules, smooth (or verruculose in SEM), rarely spinose or with low ridges, with de Bary bubbles in MLZ and Cotton Blue when dried, thin-walled to slightly thick-walled, hyaline to very pale brown. *Paraphyses* typically curved to hooked, rarely straight, sometimes with notches or swollen at the apices, septate, typically containing refractive small guttules at the apices, fading in colour and collapsed when dried. *Asci* cylindrical, operculate, 8-spored, 116–275 × 8–19 μm, with pleurorhynchous base. *Subhymenium* c. 100–150 μm thick, of dense *textura intricata*, hyphae sometimes swollen, often with scattered pigmented exudates at septa. *Medullary excipulum* 400–1500 μm thick, of *textura intricata*, hyphae cylindrical to slightly swollen, thin-walled to thick-walled, hyaline to pale brown, often with pigmented resinous exudates at septa. *Ectal excipulum* 70–150 μm thick, of *textura angularis*, less often of *textura prismatica*. Surface with warts up to 180 μm high, formed by fasciculate, short hyphoid hairs of globose to elongated cells, or of *textura globulosa-angularis* with single hyphoid hairs. Resinous exudates often present on the surface, yellow to dark brown, sometimes dissolving in MLZ, turning reddish or into brownish yellow amber drops, sometimes changing colour in KOH. *Basal mycelium* of septate, straight hyphae, that frequently branch and anastomose, turning yellow or not in KOH, often covered with pigmented, small, resinous exudates.

Ecology & Distribution — see Hansen & Olariaga (2015).

Key to species of Otidea

We were not able to study and interpret the following Chinese species and these are therefore not treated nor included in the key: *Otidea bicolor* W.Y. Zhuang & Zhu L. Yang, *O. kunmingensis* W.Y. Zhuang, *O. olivaceobrunnea* Harmaja, *O. sinensis* J.Z. Cao & L. Fan, *O. subpurpurea* W.Y. Zhuang and *O. tianshuiensis* J.Z. Cao, L. Fan & B. Liu. For *O. integra* (Bres.) Harmaja see notes under *O. phlebophora*.

1. Ascomata hypogeous, globose to subglobose, truffle-like . . . . 4. *O. subterranea*
1. Ascomata epigeous, cup-shaped to ear-shaped, split or entire 2

2. Spores ornamented 3
2. Spores smooth 5

3. Spores with fine warts ± ridges . . . . 17. *O. unicisa*
3. Spores spiny 4

4. Spores 14–17 × 7–9 μm . . . . 16. *O. kaushalii*
4. Spores 16.5–20 × 7.6–10 μm . . . . . . 18. *O. yunnanensis*

5. Spores L_m > 17 μm 6
5. Spores L_m < 17 μm 10

6. Apothecia broadly ear-shaped, split; typically ochraceous yellow to ochre orange; often associated with *Cudonia* in mossy *Picea* forests . . . . 11. *O. cantharella*
6. Apothecia cup-shaped, split or entire; brown; under *Picea* or other trees 7

7. Apothecia entire; reddish brown; basal mycelium normally with abundant minute resinous exudates; ectal excipulum hyphoid hairs often with a gelatinous sheath (more easily seen in MLZ); with *Picea* . . . . 12. *O. propinquata*
7. Apothecia split or entire; purple or ochre-brown; basal mycelium without or with sparse resinous exudates; ectal excipulum hyphoid hairs without a conspicuous sheath; with angiosperms. 8

8. Apothecia split, up to 75 mm wide; spores broadly ellipsoid to oblong, Q_m = 1.7–1.8; associated with *Fagaceae* . . . . 3. *O. platyspora*
8. Apothecia entire or split, up to 16 mm diam; spores narrowly ellipsoid to fusoid, Q_m = 1.9–2.1; most likely associated with *Betulaceae* and *Salicaceae* 9

9. Apothecia deeply cup-shaped, split; ectal excipulum without resinous exudates . . . . 1. *O. apophysata*
9. Apothecia shallowly cup-shaped, usually entire; ectal excipulum surface with abundant resinous exudates . . . . 2. *O. daliensis*

10. Receptacle surface with bright citrine yellow tones in young apothecia 11
10. Receptacle surface without citrine yellow tones 15

11. Spores Q_m = 1.7–2; apothecial base at most wrinkled, without high ribs or veins 12
11. Spores Q_m = 2–2.3; apothecial base with ribs or strongly veined at least in some apothecia 14

12. Receptacle surface ochraceous yellow; basal mycelium yellow in KOH; spores W_m = 6.5 μm, Q_m = 1.7 . . . . 25. *O. borealis*
12. Receptacle surface citrine yellow; basal mycelium unchanged in KOH; spores W_m = 5.6–6 μm, Q_m = 1.8–2 13

13. Apothecia sometimes entire, sometimes with blunt ribs at the base; North America . . . . 31. *O. oregonensis*
13. Apothecia split, without ribs at the base; Europe. . . . . 27. *O. concinna*

14. Apothecia mostly entire, base strongly ribbed-veined and anastomosing in all the apothecia . . . 32. *O. phlebophora*
14. Apothecia mostly split, base with a few ribs-veins, smooth in some apothecia . . . . 30. *O. minor*

15. At least some paraphyses straight or curved, claviform to almost capitate at apices; and/or resinous exudates of the ectal excipulum yellow or reddish yellow, turning bright yellow in KOH; apothecia split or not 16
15. Paraphyses not as such; resinous exudates of the ectal excipulum, when present, not turning bright yellow in KOH; apothecia always split 20

16. Apothecia shallowly cup-shaped and irregular, entire . . . . 29. *O. lactea*
16. Apothecia ear-shaped or deeply cup-shaped, split . . . 17

17. Paraphyses often claviform or capitate at apices, 3–9 μm broad; spores Q_m = 1.6–1.8 18
17. Paraphyses at most slightly swollen at apices, 2–5 μm broad; spores Q_m = 1.9–2 19

18. Basal mycelium turning yellow in KOH; Europe . . . . (see under *O. borealis*) *O.* sp. ‘a’

18. Basal mycelium not yellow in KOH; North America . . . . . 33. *O. rainierensis*
19. Spores L_m = 11.2–11.8 µm; sometimes receptacle with a bluish hue, ochraceous grey when dried; basal tomentum light ochre in dried specimens . . 26. *O. caeruleopruinosa*
19. Spores L_m = 10–10.6 µm; receptacle without bluish hue when fresh, reddish brown when dried; basal tomentum orange-ochre in dried specimens 28. *O. flavidobrunneola*
20. Spores L_m < 12 µm 21
20. Spores L_m > 12 µm 28
21. Apothecia dark brown with lilaceous tones; Asia . . . . 23. *O. purpurea*
21. Apothecia not dark brown, without lilaceous tones; Asia, Europe or North America 22
22. Medullary excipulum with reddish brown resinous exudates scattered among and covering some hyphae; ectal excipulum of *textura prismatica* to *textura intricata*; receptacle surface with contrasting brown warts . . . . 6. *O. papillata*
22. Medullary excipulum sometimes with yellowish brown resinous exudates at septa, not covering hyphae; ectal excipulum of *textura angularis*; receptacle surface with contrasting warts or not 23
23. At least some warts higher than 85 µm; basal tomentum orange-ochre when dried; apothecial sections often yellow in KOH; without resinous exudates at septa in the medullary excipulum . . . . 9. *O. tuomikoskii*
23. Warts up to 85 µm; basal tomentum pale ochre or yellow when dried; apothecial sections not yellow in KOH; sometimes with resinous exudates at septa in the medullary excipulum 24
24. Hymenium with distinct yellow or orange tones, ochre-yellow to pinkish orange; resinous exudates on the ectal excipulum partly dissolving into reddish grey, heterogeneous drops in KOH or basal mycelium yellow in KOH . 25
24. Hymenium without or with weak orange tones; resinous exudates sometimes turning reddish brown but not dissolving into drops in KOH; basal mycelium not turning yellow in KOH 26
25. Resinous exudates on the ectal excipulum partly dissolving into reddish grey heterogeneous drops in KOH; basal mycelium not turning yellow in KOH; North America . . . . 8. *O. pseudoleporina*
25. Resinous exudates on the ectal excipulum not dissolving into reddish grey heterogeneous drops in KOH; basal mycelium turning yellow in KOH; Asia . . . . . 19. *O. brevispora*
26. Hymenium sometimes with pink tones; apothecia yellowish ochre to brown; narrowly ear-shaped in the beginning . . . . 14. *O. nannfeldtii*
26. Hymenium without pink tones; apothecia reddish brown to orange-brown; broadly ear-shaped 27
27. Spores L_m = 10–10.7 µm; Q_m = 1.6–1.7 . . . . 13. *O. formicarum*
27. Spores L_m = 11.1–11.7 µm; Q_m = 1.7–1.9 . . . . 15. *O. subformicarum*
28. Spores Q_m < 1.8; ear-shaped 29
28. Spores Q_m > 1.8; ear- or cup-shaped 30
29. Apothecia dark brown, sometimes with olivaceous tint; paraphyses mostly with distinct notches . 10. *O. brunneoparva*
29. Apothecia cinnamon brown, without olivaceous tint; paraphyses not or slightly notched . . . . 7. *O. leporina*
30. Apothecia ochraceous yellow, hymenium often with pink tones; basal mycelium turning yellow in KOH . . . . 22. *O. onotica*
30. Apothecia pale or dark brown, without pink tones; basal mycelium not turning yellow in KOH 31
31. Receptacle medium brown; ectal excipulum resinous exudates absent or scarce, light yellowish brown; basal mycelium without dark brown resinous exudates . . . . 5. *O. alutacea* s.l.
31. Receptacle dark purple brown; ectal excipulum resinous exudates abundant, dark brown; basal mycelium with dark brown resinous exudates 32
32. Spores Q_m < 2, ellipsoid; apothecia mostly ear-shaped; North America . . . . 24. *O. smithii*
32. Spores Q_m > 2, ellipsoid-fusoid; apothecia mostly cup-shaped, split; Eurasia and North America 33
33. Receptacle strikingly purple-violaceous (fresh); medullary excipulum without, or rarely with flabellate crystal-like exudates, forming cross-like aggregates; under conifers on calcareous ground . . . . 21. *O. mirabilis*
33. Receptacle mostly without purple tones; medullary excipulum with striate exudates covering some hyphae, sometimes forming crystal-like aggregates; often under deciduous trees or on acidic ground . . . . 20. *O. bufonia*

Based on genealogical concordance phylogenetic species recognition (GCPSR: Taylor et al. 2000), using the four loci, RPB1, RPB2, EF1 and LSU rDNA, we delimited 25 species within *Otidea* (see Hansen & Olariaga 2015). In addition eight species were recognised by genetic divergence from their sisters. Twenty-eight of these are treated and discussed below, along with *O. brevispora*, *O. lactea*, *O. subterranea* and *O. yunnanensis* included in our LSU phylogeny, and *O. purpurea* that has only been studied morphologically. The species are presented following their phylogenetic relationships, inferred from our combined three- and four-gene analyses (f. 3 in Hansen & Olariaga 2015).

Otidea platyspora clade

Apothecia disc-shaped, cup-shaped and split, or globose and hypogeous, brown. Spores large, exceeding 20 µm, except 14–16.5 µm if hypogeous. Basal mycelium smooth or with very sparse resinous exudates.

Species — *Otidea apophysata*, *O. daliensis*, *O. platyspora*, *O. subterranea*.

1. ***Otidea apophysata*** (Cooke & W. Phillips) Sacc., Syll. Fung. 8: 96. 1889

Basionym. *Peziza apophysata* Cooke & W. Phillips in Cooke, Grevillea 5: 60. 1876.

≡ *Pseudotis apophysata* (Cooke & W. Phillips) Boud., Hist. Classific. Discomyc. Europe: 52. 1907.

Holotype. ENGLAND, Shrewsbury, in a damp ditch, 1876, *W. Phillips* (K(M) 30410 ex Herb. Phillips). *Isotype* (K(M) 167215 ex Herb. Cooke) !

Misapplied names

– *Otidea felina* sensu Boudier, Icon. Mycol. livr. 29: n°. 512, pl. 331. 1910 (preliminary text with 'circulaires').

Apothecia solitary to caespitose, 8–30 mm high, up to 15 mm wide, initially ear-shaped, then soon expanding and becoming cup-shaped, split, sessile or stipitate. *Hymenium* purple brown (6D3, 6D4), when dried dark orange brown (6E7, 6F7). *Receptacle surface* pale greyish orange (6C5), purple brown (6D4), when dried dark orange brown (6E7, 6F7), furfuraceous. Warts scarce to absent, low. *Stipe* absent. *Basal tomentum and mycelium* whitish to pale orange grey (5B2). *Spores* narrowly ellipsoid to fusoid, narrowing toward the poles, sometimes inequilateral, with two large guttules, and often with several smaller guttules, smooth, hyaline, 20–24.5 × 9–11 µm (L_m = 21.6 µm, W_m = 10 µm, Q_m = 2.1; n = 1). *Paraphyses* curved to hooked, seldom straight, slightly enlarged at apices, 3–4(–5) µm wide, sometimes with a sinuous underside or with 1–2 notches, frequently branching, entangled and interconnected, when dried containing small, refractive, hyaline guttules. *Asci* 172–197 × 12–13 µm. *Apothecial section* 700–850 µm thick. *Medullary excipulum* of *textura intricata*, 400–500 µm thick, hyphae slightly thick-walled, 5–9 µm wide, pale brown. *Ectal excipulum* of *textura angularis*, 70–110 µm, cells thin-walled, yellowish brown, 18–33 × 13–22 µm. Surface with low warts, up to 40 µm high, cells ovoid to globose, constricted at septa, 8–13 µm wide. Resinous exudates absent. *Basal mycelium* of 4–5 µm broad, pale brown hyphae, sometimes with oily refractive drops on the surface.

Specimens examined. Germany, Nordrhein, Herten, 1 Sept. 1999, *F. Kasparek*, private herb. Kasparek s.n. (dupl. S-F257062).

Notes — *Otidea apophysata* is characterised by deeply cup-shaped, split, brown apothecia, and large, ellipsoid to fusoid spores. *Otidea daliensis* is a closely related species, distinguished by darker brown, shallowly cup-shaped, usually entire apothecia, and abundant dark brown resinous exudates on the outermost cells of the ectal excipulum. *Otidea platyspora* has also brown apothecia and large spores, but it differs from *O. apophysata* in the larger apothecia, partly buried in the substrate, broadly ellipsoid to oblong spores, and non-entangled paraphyses without notches.

The name *O. apophysata* has been misapplied twice for *O. daliensis* (Boudier 1909b, Pérez-Butrón & Fernández-Vicente 2008). The type material of *O. apophysata* lacks resinous exudates on the ectal excipulum, which clearly distinguishes it from *O. daliensis*. An original painting by W. Phillips, based on the type material of *O. apophysata* and preserved at RBG Kew (reproduced in Parslow & Spooner 2013), shows typical brown, split, deeply cup-shaped apothecia. The illustration by Cooke (1878, f. 350), based on drawings and (likely dried) specimens communicated by W. Phillips, shows slightly darker apothecia than typical.

Otidea apophysata is only known from very few reports from France (Boudier 1910 as *O. felina*), Germany (Häffner & Winterhoff 1989, Kasparek 2000), Belgium and Spain (Van Vooren 2011a). In Mid to South Britain it is widely distributed, with collections from fourteen different localities (Parslow & Spooner 2013). Unlike most *Otidea* species, *O. apophysata* shows preference for damp habitats, and might be associated with *Alnus* and *Populus* (Häffner & Winterhoff 1989, Parslow & Spooner 2013).

2. ***Otidea daliensis*** W.Y. Zhuang & Korf, Mycotaxon 35: 300. 1989

Holotype. China, Yunnan, Dali, Hudiequan Park, alt. 2100 m, on bare soil under seedlings of *Plantago major*, 5 Nov. 1988, *R.P. Korf*, *L.S. Wang & W.Y. Zhuang* (HMAS 57688). *Isotype* (CUP-CH 2532).

Misapplied names
– *Pseudotis apophysata* sensu Boudier, Icon. Mycol. livr. 24: n°. 471, pl. 332. 1909 (preliminary text with ‘circulaires’).
– *Otidea apophysata* sensu Pérez-Butrón & Fernández-Vicente, Errotari 5: 37. 2008.

Apothecia gregarious, up to 9 mm high, 3–16 mm wide, initially cup-shaped, sometimes split, then becoming shallowly cup-shaped, sessile or stipitate. *Hymenium* when dried dark purple brown (7F5, 7F6) to dark brown (6F5). *Receptacle surface* dark purple brown (7F5, 7F6), when dried dark brown (6F5), furfuraceous. Warts absent or very low. *Stipe* if present very short. *Basal tomentum and mycelium* whitish to pale orange grey (5B2). *Spores* broadly ellipsoid to ellipsoid and narrowing toward the poles, sometimes inequilateral, with two large guttules, and often with several smaller granules, smooth, hyaline, (19.5–)20.5–23 × 10.5–12(–13) µm (L_m = 21.2–21.5 µm, W_m = 10.7–11 µm, Q_m = 1.9–2.1; n = 2). *Paraphyses* curved to hooked, sometimes slightly enlarged at apices, 2.5–3.5(–5) µm wide, sometimes with slightly swollen areas, apices sometimes embedded in a brown matter, when dried containing small, refractive, brown guttules. *Asci* 199–212 × 15–17 µm. *Apothecial section* 600–850 µm thick. *Subhymenium* c. 90–110 µm thick, of dense *textura intricata*, visible as a darker zone, cells cylindrical to swollen, with scattered brown resinous exudates at septa. *Medullary excipulum* of *textura intricata*, 300–400 µm thick, hyphae 4–6.5 µm wide, slightly thick-walled, pale brown, with brown resinous exudates at septa. *Ectal excipulum* of *textura angularis*, 90–120 µm thick, cells thin-walled, yellowish brown, 18–28 × 11–28 µm. Surface with broadly conical warts. Non-warted parts with 2–5-celled hyphoid hairs, with claviform uppermost cell, more rarely cylindrical, constricted at septa, 6–9 µm wide. Resinous exudates abundant, dark brown, partly dissolving in MLZ. *Basal mycelium* of 3.5–4 µm wide, hyaline hyphae, with yellowish brown, small, resinous exudates.

Specimens examined. France, 1869, *L. Quélet* (UPS F-629790). – Spain, Basque Country, Bizkaia, Galdames, Presa de Aguas Juntas, sandy soil under *Populus nigra*, 11 Aug. 2003, *J.L. Pérez Butrón*, SEST-03071103; 17 Aug. 2006, SEST-06081702.

Notes — *Otidea daliensis* is recognised by small, usually entire, dark purple brown, shallowly cup-shaped apothecia, large ellipsoid spores often narrowing toward the poles, and abundant brown resinous exudates on the ectal excipulum. This species has been confused with *O. apophysata* (see *O. apophysata*).

The first known report of *O. daliensis* was by Boudier (1909b), as *Pseudotis apophysata*. The plate 332 (n°. 471) shows the typical dark purple, shallowly cup-shaped apothecia, in contrast to *O. apophysata*, depicted in plate 331 (n°. 512) as *O. felina* (Boudier 1910). Mornand & Courtecuisse (2005) proposed a provisional name, *O. boudieri*, for the Boudier *P. apophysata* plate (= *O. daliensis*, n°. 332). Zhuang & Korf (1989) described *O. daliensis* without comparing it to *O. apophysata*. Material with small, shallowly cup-shaped apothecia and darker colour was reported from the Iberian Peninsula as *O. apophysata* (Pérez-Butrón & Fernández-Vicente 2008), and thus had similarities with *O. daliensis* and Boudier’s plate 332. Van Vooren (2011a) considered the Iberian *O. apophysata* material to represent *O. daliensis*. After restudying the Iberian material and comparing it to *O. apophysata*, we agree with that statement. LSU sequences obtained from the Iberian material and from the Chinese holotype of *O. daliensis* are identical.

3. ***Otidea platyspora*** Nannf., Ann. Bot. Fenn. 3: 317. 1966. — Fig. 7

Holotype. Sweden, Uppland, Djursholm, Oct. 1951, *A. Zander*, Fungi Exs. Suec. 3284 (UPS F-005428). *Isotype* (S-F88395) !

Misapplied names
– *Otidea cochleata* sensu Boudier, Icon. Mycol. livr. 21: n°. 461, pl. 329. 1908 (preliminary text with ‘circulaires’).

Apothecia caespitose, 60–70 mm high, 40–75 mm wide, initially ear-shaped, then soon expanding and becoming deeply cup-shaped, split, sessile or shortly stipitate. *Hymenium* initially yellowish brown (5C6, 5C7), pale greyish brown (5C3, 5C4) to dark brown (6F3–6F6), when bruised margin blackish, when dried brownish ochre (5B4, 5B5). *Receptacle surface* dark ochre brown (5D7, 5D8), slightly hygrophanous, in drying pale ochre brown (5B6), when dried yellowish brown (5C6, 5C7), sometimes wrinkled at the base, finely furfuraceous in the margin. Warts absent. *Stipe* not well developed. *Basal tomentum and mycelium* whitish to pale brown (5A3). *Spores* broadly ellipsoid

Fig. 7 *Otidea platyspora**. a. Apothecia; b. spores; c. paraphyses; d. ectal excipulum (a: KH.10.183; b–d: KH.09.163). — Scale bars = 10 µm; * = all fresh material.

to oblong, rarely slightly inequilateral, with two large guttules, often with several smaller guttules, smooth, hyaline, 18–22 × (9.5–)10.5–12 µm (L_m = 19.8–20.7 µm, W_m = 10.9–11.6 µm, Q_m = 1.7–1.8; n = 6). *Paraphyses* curved to hooked, of the same width or slightly enlarged at apices, 2.5–3.5(–5) µm wide, without notches, rarely with a slightly swollen area on the underside, when fresh containing small, refractive, light brownish yellow guttules; when dried tiny, light yellow granules. *Asci* 168–213 × 14–19 µm. *Apothecial section* 700–1700 µm thick. *Subhymenium* 80–100 µm thick, visible as a darker zone, cells cylindrical, densely arranged, with scarce yellowish brown resinous exudates at septa. *Medullary excipulum* of *textura intricata*, 550–1100 µm thick, hyphae 3.5–10 µm wide, sometimes slightly swollen, thin-walled, light yellowish brown. *Ectal excipulum* of *textura angularis*, 70–90 µm, cells thin-walled, pale brown, 13–37 × 12–22 µm. Surface with hyphoid hairs, 33–70 µm long, of 4–7 ovoid to subglobose cells, constricted at septa, 6–9 µm wide, sometimes with a light brown matter. Resinous exudates absent to scarce, pale brown, dissolving in MLZ. *Basal mycelium* of 3.5–4.5 µm wide, hyaline to very pale brown hyphae, sometimes with oily refractive drops on the surface, sometimes with minute bipyramidal resinous exudates.

Specimens examined. Azerbaijan, Montes Talysh, in silva mixta, 14 Oct. 1962, *E. Parmasto* (UPS F-629452). – Denmark, East Jylland, Kammerherrens Ege, Moesgård Skov, S of Århus, under *Fagus* and *Quercus*, 11 Sept. 2006, *J. Vesterholt*, JV06-656 (C). – France, Ain, commune de Saint-Benoit, forêt d´Évieu, under *Quercus robur*, *Carpinus betulus*, *Corylus avellana* and *Alnus glutinosa*, 15 July 2011, *F. Armada*, NV 2011.07.04 (dupl. S). – Sweden, Uppland, Stockholm, Drottningsholm, under *Quercus robur*, 13 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.163 (S); Uppland, Stockholm, Solna, Karlbergsparken, garden with broadleaf trees, 29 July 2006, *H.-G. Toresson* (S-F248339); Uppland, Stockholm, Sånga, Svartsjö slott, under *Quercus*, *Fagus* and *Corylus*, 31 Aug. 2008, *H. Kauffman*, HK08046 (S); Uppland, Uppsala, mixed forest with *Pinus sylvestris*, *Picea abies*, *Betula pendula* and *Quercus robur*, 9 Oct. 2011, *J.C. Zamora* (BIO-Fungi 16391); Uppland, Uppsala, Hågadalen-Nåsten Nature Reserve, Predikstolen, under *Corylus*, *Populus*, *Quercus* and *Picea*, on rich ground, 6 Sept. 2010, *K. Hansen & I. Olariaga*, KH.10.183 (S).

Notes — *Otidea platyspora* is characterised by large, caespitose, brown apothecia, blackening in bruised margins and large spores. Macroscopically it resembles members of the *O. alutacea* complex, but these differ in the smaller spores. *Otidea apophysata* and *O. daliensis* have likewise brown apothecia and large spores, but can be distinguished by having even larger spores and smaller (up to 30 mm) apothecia (see further under those species).

Otidea platyspora is a striking species with scarce records. It was described from Sweden and has been reported from France (Boudier 1908, Nannfeldt 1966, Van Vooren & Armada 2011), the Netherlands (Maas Geesteranus 1967) and recently from Britain and Denmark (Parslow & Spooner 2013). We report it as new from Azerbaijan and give additional records from Denmark and Sweden. *Otidea platyspora* appears to have been overlooked and is more widespread than thought previously.

4. ***Otidea subterranea*** Healy & M.E. Sm. in Smith & Healy, Mycol. Res. 113: 860. 2009

Holotype. USA, Iowa, Ledges State Park, shallowly hypogeous, erumpent on soil, 30 Aug. 1997, *R. Healy* RH69 (FH).

Notes — *Otidea subterranea* is the only known hypogeous species of *Otidea*. The pustules (c. 50–100 µm high) on the outer surface of the ptychothecia and the incrusted tomentum are typical for *Otidea*. The asci are cylindrical, with 8 uniseriate spores, placed in a defined hymenium. Unlike most *Otidea* species the spores are uniguttulate. As an adaptation to a hypogeous habit active spore discharge has been lost. Probably for the same reason, the paraphyses are aggregated and fused subapically to form an epithecium of brown thick-walled cells, and are reminiscent of the frequently branching, entangled and interconnected paraphyses in *O. apophysata*. There are no other morphological features that support the exact placement of *O. subterranea* in the *O. platyspora* clade. The receptacle surface of *O. subterranea* ascomata is whitish to cream in young and peach-cream to buff with tan-brown areas in older specimens. The gleba is of dark brown fertile veins lined with a thin, light yellowish brown hypothecium, but the sterile veins are of whitish hyphae (Smith & Healy 2009).

Otidea alutacea clade

Apothecia cup-shaped and split, brown. Spores typically ellipsoid, with almost parallel sides. Outermost ectal excipulum and basal mycelium smooth or with very sparse resinous exudates.

Species — *Otidea alutacea* s.l.

5. *Otidea alutacea* (Pers.) Massee, Brit. Fungus-Fl. 4: 446. 1895. — Fig. 8

Basionym. *Peziza alutacea* Pers., Observ. Mycol. 2: 78. 1799; non *Peziza alutacea* Schumach., Enum. Pl. 2: 431. 1803 (homonym).

≡ *Scodellina alutacea* (Pers.) Gray, Nat. Arr. Brit. Pl. 1: 668. 1821.

≡ *Peziza cochleata* var. *alutacea* (Pers.) Fr., Syst. Mycol. 2: 50. 1822: Fr. loc. cit. (‘ß *alutacea*’).

≡ *Plicaria alutacea* (Pers.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 327. 1870.

≡ *Aleuria alutacea* (Pers.) Gillet, Champ. France Discom. 1: 42. 1879.

Lectotype. Bull., Hist. Champ. France 1: t. 154, f. b., designated by Carbone (2010a). *Epitype*. (L0111551, Herb. Persoon), designated by Carbone (2010a).

[1]*Apothecia* gregarious, rarely caespitose, 15–75 mm high, 8–48 mm wide, initially ear-shaped, soon expanding, becoming shallowly to deeply cup-shaped, split, sessile or stipitate. *Hymenium* initially brown (5D6), then yellowish brown (5D4, 5D5) to dark reddish brown (7D7, 7E7), when dried purple brown (6D6, 6D7). *Receptacle surface* slightly hygrophanous, in drying yellowish brown (5D5, 5D6), or sometimes with purplish brown (7D5) tones, when dried light ochre (5A4, 5B4) brownish ochre (5B5, 5B6), finely furfuraceous to slightly warty in the margin. Warts flattened, gregarious, concolorous, darker when the outside in drying. *Stipe* 3–6 × 3–4 mm. *Basal tomentum and mycelium* white to very light ochre (5A2). *Spores* ellipsoid to broadly ellipsoid, oblong ellipsoid, slightly inequilateral, with two large guttules, often with several smaller granules, smooth, hyaline, (13.5–)14.5–16.5(–17.5) × 6.5–7.5(–8) µm (L_m = 14.6–16.1 µm, W_m = 6.6–7.5 µm, Q_m = 2.1–2.2; n = 5). *Paraphyses* curved to hooked, only few straight, of the same width or slightly enlarged at apices, 2.5–4.5 µm wide, without notches, sometimes embedded in a brown matter at apices, when fresh containing small, refractive, light brownish yellow guttules; when dried brownish yellow. *Asci* 140–187 × 11–13 µm. *Apothecial section* 750–1050 µm thick. *Subhymenium* c. 80–100 µm thick, visible as a darker zone, cells cylindrical to swollen, densely arranged, with scattered yellowish brown resinous exudates at the septa. *Medullary excipulum* of *textura intricata*, 400–650 µm thick, hyphae thin-walled to slightly thick-walled, 4–9 µm wide, hyaline to light brown, sometimes with yellowish brown resinous exudates at septa. *Ectal excipulum* of *textura angularis* of 80–100 µm, cells thin-walled, pale brown, 9–21 × 9–17 µm. Surface with broad conical warts, 35–57 µm high, formed by short, fasciculate, hyphoid hairs, of 6–7 globose to subglobose cells, constricted at septa, 7–10 µm wide. Resinous exudates absent to scarce, yellowish brown, dissolving in MLZ. *Basal mycelium* of 3–4.5 µm wide, hyaline hyphae, with oily refractive drops on the surface, sometimes with minute resinous exudates.

Specimens examined. ***O. alutacea* s.str.** — Denmark, S Sjælland, Møn, Store Klinteskov, by Svantestenen, on calcareous soil (pH 7.0) along forest road, under deciduous trees, together with *Humaria hemisphaerica* and *Trichophaea woolhopeia*, 11 Sept. 1994, *K. Hansen & S.K. Sandal*, KS-94-111 (C). – France, Puy-de-Dôme, Auvergne, Nadayat, sous feuillus en terrain neutrocline, 20 Sept. 1998, *G. Corriol*, GC 98092002 (dupl. S). – Italy, Piemonte, Vignole Borbera (AL), Fraz. Variano superiore, under *Quercus pubescens* and *Castanea sativa*, 19 Oct. 2010, *M. Carbone* (S-F257084). – Norway, Nord-Trøndelag, Leksvik, Gjøråsvika, on rich, bare ground, under *Corylus* and *Picea*, on a steep slope, 3 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.133 (S). – Spain, Gipuzkoa, Tolosa, Elosegi markesaren lorategiak, under broadleaf trees in a garden, 29 May 2009, *J.I. López-Amiano*, JLA 2009052902 (ARAN-Fungi A3023204). – Sweden, Gotland, Ollajvs Nature Reserve, close to Ljugarn, under *Picea* and *Pinus* on calcareous ground, 27 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.278 (S). **Clade 1** — Denmark, Eastern Falster, Korselitze-forests, 5 Oct. 2007, *H. Knudsen*, KH.07.46 (S). – Sweden, Uppland, Stockholm, Norra Järvafältet, Hansta Nature Reserve, on rich ground under *Corylus* and *Quercus*, 8 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.193 (S); Uppland, Stockholm, N Djurgården, Stora skuggan, on soil in grazed open oak forest, 12 Sept. 2008, *J. Santos*, JS.08.81 (S); Uppland, Uppsala, Hågadalen-Nåsten Nature Reserve, Predikstolen, under *Quercus robur*, *Picea abies*, *Corylus* and *Salix*, on rich bare ground, 17 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.170 (S). **Clade 2** — USA, Oregon, Lincoln Co., Devil’s Punchbowl State Park, 13 Mar. 1997, *E.T. Peterson* (OSC 56770); Washington, Pierce Co., Mt Rainier National Park, Lower Tahoma Creek, under *Pseudotsuga*, *Tsuga*, *Picea* and *Calocedrus*, 29 Oct. 1996, *E.T. Peterson* (OSC 56747); ibid., 30 Oct. 1996 (OSC 56754); ibid., 18 Oct. 1997 (OSC 56798); Washington, Snohomish Co., Sloan Creek trail, 24 Sept. 1997, *E.T. Peterson* (OSC 56777). **Clade 3a** — Norway, Nord-Trøndelag, Leksvik, Gjøråsvika, on slope under *Corylus* and *Picea*, on rich ground, 3 Sept. 2009, *V. Kučera & I. Kautmanová*, KH.09.135 (S). – Sweden, Södermanland, Nynäshamn, Herrhamra, on soil under *Fagus*, in narrow forest area along the road, 19 Sept. 2013, *K. Hansen & X.H. Wang*, KH.13.50 (S); Uppland, Norrtälje, Länna, under *Corylus*, 26 Aug. 2008, *J. Santos*, JS.08.43 (S); Uppland, Uppsala, Hågadalen-Nåsten Nature Reserve, Predikstolen, under *Quercus robur*, *Picea abies*, *Corylus* and *Salix*, on rich, bare ground, 6 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.198 (S). **Clade 3b** — Denmark, S Sjælland, Møn, Store Klinteskov, Vestre Ulvemose, on calcareous soil in deciduous forest, 26 Sept. 1994, *K. Hansen & S.K. Sandal*, KS-94-192 (C). – Sweden, Uppland, Uppsala, Hågadalen-Nåsten Nature Reserve, Predikstolen, under *Corylus*, *Populus* and *Picea*, on rich ground, 19 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.178 (S). **Clade 4** — USA, Oregon, Benton Co., Corvallis, McDonald-Dunn Research Forest, 10 Oct. 1997, *E.T. Peterson* (OSC 56782); ibid., 18 Nov. 1996 (OSC 56758); Oregon, Benton Co., Corvallis, west side of NW Beechwood Place, scattered to clustered on rotting bark mulch and in thin grass under *Pseudotsuga menziesii*, 17 Nov. 2010, *N.S. Weber*, NSW10200 (OSC 150345); Oregon, Corvallis, Witham Hill, 25 Nov. 1997, *E.T. Peterson* (OSC 56813); Oregon, Douglas Co., 20 Oct. 2010, *J. Moore*, Moorefun 19 (OSC); Oregon, Douglas Co., Bear Gulch, under *Pseudotsuga menziesii*, 13 Jan. 1999, *R. Davidson* (OSC 67524); Oregon, Douglas Co., Slimewater, under *Pseudotsuga menziesii*, *Quercus garryana*, *Abies grandis*, etc., 12 Sept. 1999, *Frymire* (OSC 72978); Oregon, Douglas Co., Umpqua, under *Pseudotsuga menziesii*, *Abies concolor*, *Calocedrus decurrens*, *Corylus cornuta*, etc., 23 Mar. 2000, *E. Stewart* (OSC 72979); under *Pseudotsuga menziesii*, *Pinus ponderosa*, *Calocedrus decurrens*, *Pinus lambertiana*, *Abies concolor*, etc., 15 Dec. 1999, *C. Rusch* (OSC 72176); Oregon, Lane Co., Willamette National Forest, Middle Fork Ranger District, under *Tsuga heterophylla*, *Thuja plicata* and *Abies grandis*, 18 Nov. 2002, *Smith* (OSC 119567).

Additional material of O. alutacea s.l. Denmark, Sjælland, Hareskoven, N of Copenhagen, 2 Aug. 1961, *H. Dissing* (C-F-48301). – France, Orliénas, sous *Quercus* et *Cedrus atlantica*, 13 Nov. 2008, *B. Rivoire & N. Van Vooren*, NV 2008.11.01 (dupl. S-F256976); Rhône, Bron, Parc de Parilly, 24 Sept. 2008, *J. Cavet*, NV 2008.09.32 (dupl. S-F256974); Rhône, Courzieu, hameau des Verchères, sous *Pseudotsuga menziesii*, 26 Oct. 2008, *D. Carbonnel*, NV 2008.10.02 (dupl. S-F256975). – Italy, Puglia, Mesagne (BR), Bosco Lucci, in soil, mainly under *Quercus ilex*, 12 Oct. 2010, *M. Carbone* (S-F257085). – Norway, Nord-Trøndelag, Leksvik, Gjøråsvika, mixed forest on rich ground,

---

[1] Description based only on specimens of *O. alutacea* s.str.

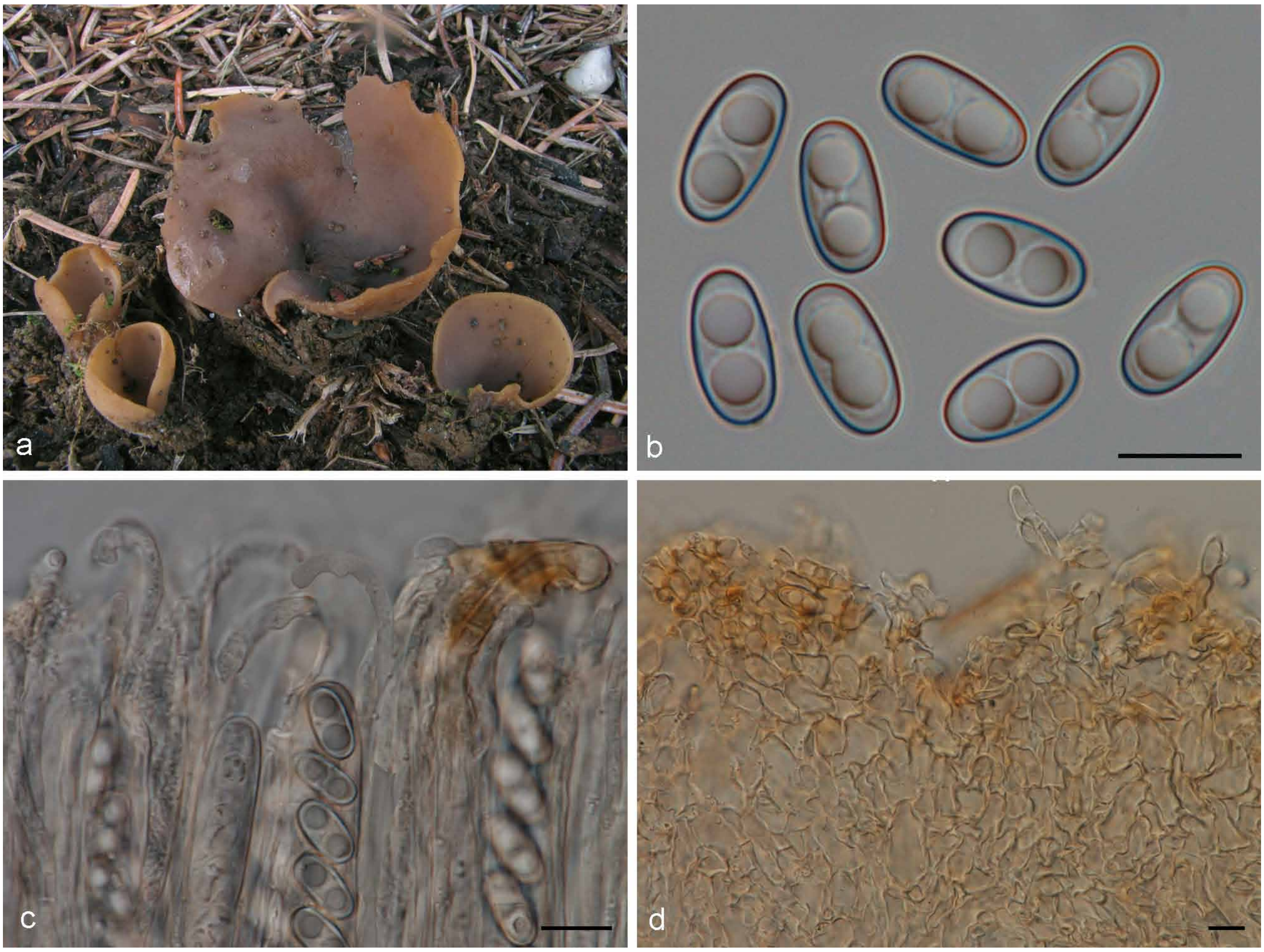

Fig. 8 *Otidea alutacea* s.str. (KH.09.133). a. Apothecia; b. spores in water†; c. paraphyses in water†; d. ectal excipulum in KOH†. — Scale bars = 10 µm; † = dried material.

3 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.137 (S); ibid., *R. Braathen*, KH.09.139 (S); Nordland, Rana, Rausandaksla, in salico-betuletum, on limestone, 21 Sept. 1974, *S. Sivertsen* (C-F-60697). – Spain, Madrid, Arboreto de ETSI Montes, under *Quercus suber*, *Pinus pinea* and *Nerium oleander*, 21 Nov. 2006, *L. Rubio Casas* (AH42204). – Sweden, Gotland, near Visby, Värnhem, on rich ground under *Fagus* and *Quercus*, with *Hepatica nobilis*, 22 Sept. 2009, *E. Bohus-Jensen*, *K. Hansen & I. Olariaga*, KH.09.187 (S); Gästrikland, Hofors, Sibbersbovägen, on rich ground under *Corylus*, 1 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.154 (S); Jämtland, Ändsjön Nature Reserve, in rich *Picea* forest, 26 Aug. 2009, *H. Lindström*, KH.09.97 (S); Närke, Ekeby, Kvarntorp, under a big *Quercus* by the road, 10 Sept. 2008, *J. Santos & K. Hansen*, JS.08.57 (S); Närke, Tysslinge, Latorpsbruk, Grytsätterskogen, grassland with *Quercus*, 13 Sept. 2008, JS.08.76 (S); Närke, Örebro, Hästhagen, by Svartån, mixed forest, 13 Sept. 2008, *H. Kauffman*, JS.08.74 (S); Skåne, Helsingborg, Fredriksdals Friluftmuseum, 16 Sept. 2010, *G. Hamilton*, KH.10.206 (S); Skåne, Kjugekull Nature Reserve, on bare ground under *Quercus rubra*, *Corylus* and *Fagus*, 24 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.262 (S); Skåne, Maltesholm, forest close to the castle, on the ground under *Fagus*, close to *Alnus*, 25 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.265 (S); Torne Lappmark, Abisko, 12 Aug. 1974, *M.D. Paulsen & N. Tams* (C-F-48045); Uppland, Stockholm, Enebyberg, Rinkebyskogen, on bare soil in a ditch, under *Picea*, *Betula* and *Populus*, 28 Aug. 2008, *J. Santos*, JS.08.50 (S); ibid., in deciduous forest under *Corylus*, but also *Tilia*, *Quercus* and *Betula*, 1 Sept. 2008, *J. Santos*, JS.08.56 (S); Uppland, Stockholm, Norra Järvafältet, Hansta Nature Reserve, on naked soil among leaves, under large *Corylus*, also *Quercus*, 8 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.189 (S); Uppland, Uppsala, Hågadalen-Nåsten Nature Reserve, Predikstolen, on rich ground under *Quercus*, *Corylus*, *Populus tremula* and *Picea*, 17 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.173 (S).

Notes — We consider *O. alutacea* s.l. to comprise a species complex. It is recognised by the medium brown, cup-shaped, split apothecia, an ectal excipulum with only sparse resinous exudates if any, and predominantly oblong spores. Although sometimes treated as a well-delimited species (Harmaja 2009a), spore sizes of *O. alutacea* provided by different authors vary considerably, e.g. 14–16 × 7–9 µm (Dissing 2000) or 12.5–14.5 × 6.2–7.3 µm (Harmaja 2009a). In fact, *O. cochleata* has been separated from *O. alutacea* on account of larger spores, 16–18 × 7–8 µm (Dissing 2000), or darker apothecia (Mornand & Courtecuisse 2005, Liu & Zhuang 2006, Zhuang 2006). Meanwhile, two taxa of the *O. alutacea* species complex have been separated in North America, based on apothecia colour, and spore size and shape (Peterson 1998). Our LSU phylogeny resolved several clades within *O. alutacea* s.l. (Fig. 1), which are strongly supported in our multigene phylogeny (Hansen & Olariaga 2015). It appears that the spore sizes within each clade have a fairly narrow range, but overlap exists between the clades. Patterns of continental speciation are suggested as well; two clades have North American specimens (clade 2, 4), and the rest contain samples from Europe and Asia.

Carbone (2010a) selected a lectotype and an epitype for *O. alutacea*. A spore range of 15.5–17 × 7 µm was given for the epitype specimen (Carbone 2010a), and based on this we assign *O. alutacea* s.str. to the clade inferred from the phylogenetic analyses encompassing this spore size. The description above is based solely on the specimens of that clade, which are characterised by the initially shallowly cup-shaped apothecia, with rather light ochraceous brown hymenium, which later becomes purple brown and more deeply cup-shaped. The lectotypification of *O. alutacea* proposed by Parslow & Spooner (2013) is superfluous.

Among the Eurasian clades, clade 1 contains North European specimens characterised by small spores (12–13.5 × 5.5–7 µm, L_m = 12.2–12.9 µm, W_m = 5.8–6.6 µm, Q_m = 1.9–2.2), non-overlapping with *O. alutacea* s.str. and clade 3. Clade 1 should be compared to *O. kunmingensis*, a taxon belonging to the *O. alutacea* complex characterised by short spores (Zhuang & Yang 2008). Clade 3a encompasses three specimens with spores sizes 13.5–15 × 6.5–8 µm (L_m = 14.5–14.6 µm, W_m = 6.7–7.3 µm, Q_m = 2–2.2) overlapping with those of *O. alutacea* s.str. as described here. The apothecia differ slightly macroscopically from *O. alutacea* s.str. in being deeply cup-shaped in the beginning, reddish brown when young, later pale ochre-brown. Clade 3b is composed of two collections with larger spores, 15.5–17.5 × 7.5–8 µm (L_m = 16.1–17.4 µm, W_m = 7.7–8 µm, Q_m = 2–2.3), but slightly overlapping with *O. alutacea* s.str. and clade 3a. Clade 3b may correspond to *O. cochleata* sensu Dissing (2000). The two North American clades (2 and 4) comprise specimens with clearly non-overlapping spore sizes, 15–18 × 7–8 µm (L_m = 15.5–16.9 µm, W_m = 7.3–7.9 µm, Q_m = 2–2.2) and 12–14.5 × 6.5–8.5 µm (L_m = 12.5–14 µm, W_m = 6.6–7.5 µm, Q_m = 1.8–2), respectively. These two clades correspond to the two species distinguished by Peterson (1998) in Western North America, as *O. alutacea* (clade 2) and *O. umbrina* (clade 4). These species were said to differ in colour of fresh apothecia. Clades 2 and 4 have spores that overlap with European clades, and it is so far problematic to distinguish them using only morphology and disregarding the geographical origin.

To be able to fully clarify species boundaries within the *O. alutacea* complex, sampling of additional collections for molecular study is needed. Distinguishing morphological and ecological characters should be sought, especially through studying fresh

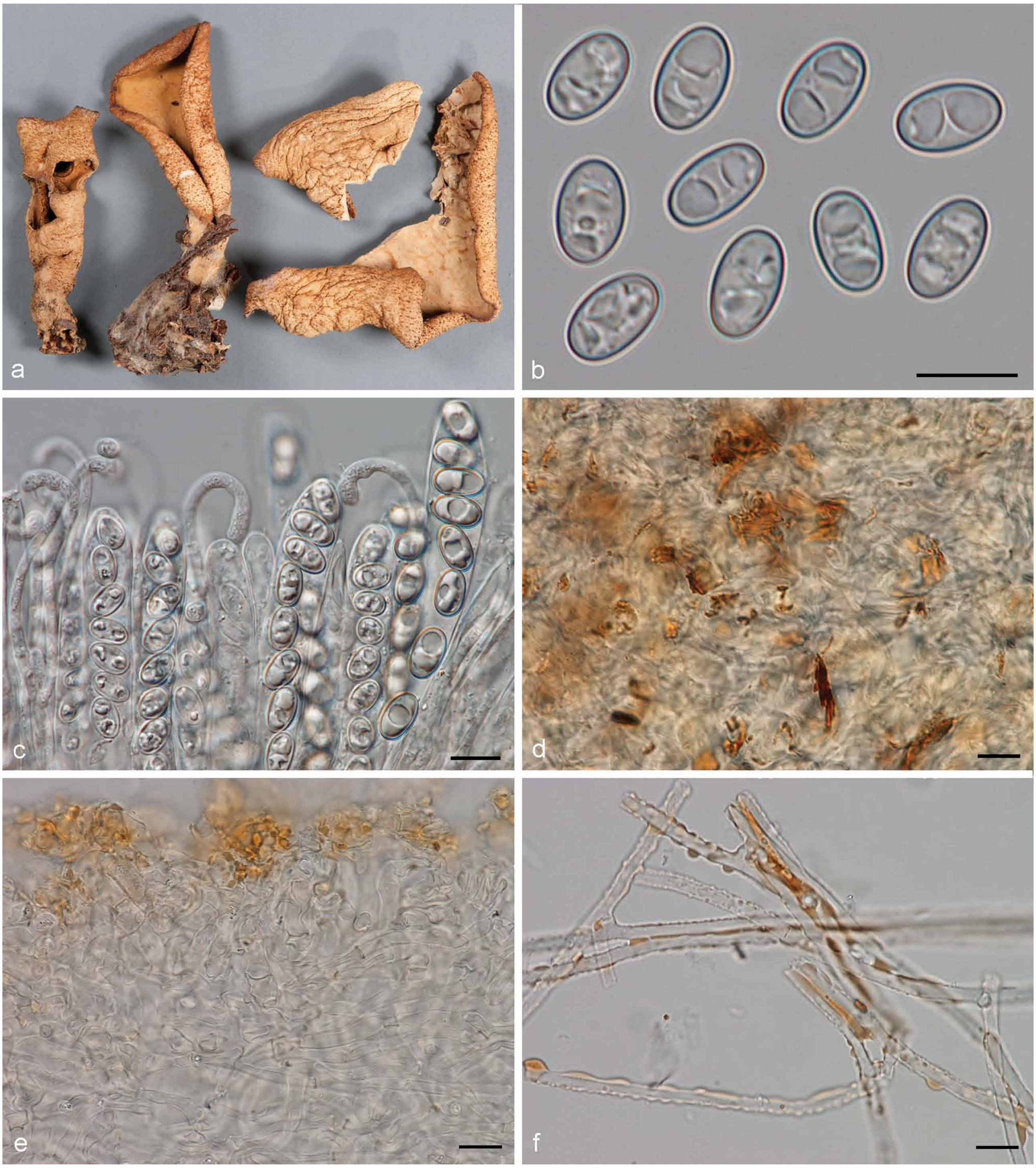

Fig. 9 *Otidea papillata*†. a. Apothecia; b. spores in water; c. paraphyses; d. resinous exudates in the medullary excipulum in water; e. ectal excipulum in KOH; f. basal mycelium in KOH (a–d, f: H6003547, holotype; e: TUR 102134). — Scale bars = 10 µm; † = all dried material. — Photos: a. J. Kearey.

material. Several names that belong to this complex, such as *O. alba*, *O. cinerascens*, *O. cochleata*, *O. felina* and *O. kunmingensis* should be considered as this study is undertaken.

Otidea papillata clade

Apothecia cup-shaped, split. Receptacle surface with contrasting warts. Spores small, 9.5–11 µm. Medullary excipulum with brown resinous exudates embedding some hyphae. Ectal excipulum poorly differentiated, of *textura prismatica* to *textura intricata*. Resinous exudates on the ectal excipulum not dissolving in MLZ.

Species — *Otidea papillata*.

6. *Otidea papillata* Harmaja, Karstenia 15: 31. 1976 — Fig. 9

Holotype. Finland, Kainuu, Paltamo, Melalahti, Myllymäki, predominantly coniferous grass-herb forest on distinctly calcareous soil, in litter mainly composed of spruce needles, 23 Sept. 1971, *H. Harmaja* (H6003547) !

Apothecia 23–30 mm high, 7–33 mm wide, initially broadly ear-shaped, with upper margin rounded, then becoming cup-shaped, split, stipitate or sessile. *Hymenium* ochre (5B5, 5B6) to yellowish ochre (4A5) when dried. *Receptacle surface* yellowish brown (5C6, 5C7) when dried, warty. Warts conical, angular or rounded, gregarious, distinctly darker than the background, dark ochre brown to brown. *Stipe* 7–10 × 3–4 mm. *Basal tomentum and mycelium* abundant, pale brownish ochre (5A3) to orange-ochre (6A3). *Spores* broadly ellipsoid, seldom very slightly inequilateral, with two large guttules, smooth, hyaline, 9.5–11(–11.5) × 5.5–6.5 µm (L_m = 10–10.7 µm, W_m = 6.1–6.3 µm, Q_m = 1.6–1.7; n = 2). *Paraphyses* curved to tightly hooked, usually enlarged at apices, 3–4 µm wide, sometimes with 1–2 shallow notches, sometimes truncate or forked at apices, when dried containing small, refractive, hyaline granules. *Asci* 116–165 × 9–10.5 µm. *Apothecial section* 900–1200 µm thick. *Subhymenium* 70–90 µm thick, of dense *textura intricata*, visible as a pale brown zone. *Medullary excipulum* of *textura intricata*, 600–800 µm thick, hyphae 5.5–10.5 µm wide, thin-walled to slightly thick-walled, hyaline to very pale yellow, with brown resinous exudates scattered among and covering some hyphae, sometimes rod-shaped, paler and partially dissolving in KOH. *Ectal excipulum* of *textura prismatica* to *textura intricata*, 70–100 µm, cells thin-walled, hyaline, 13–35 × 9–18 µm. Surface with conical to rounded warts, 65–100 µm high, formed by short, fasciculate, hyphoid hairs, sometimes with a gelatinous sheath. Resinous exudates abundant, yellowish brown to reddish brown, paler in KOH, not dissolving in MLZ. *Basal mycelium* of 2.5–4.5(–6) µm wide, septate, hyaline to very pale yellow hyphae, unchanged in KOH, smooth or with regularly arranged, spheroid, yellow, resinous exudates, sometimes embedded in a yellowish matter, dissolving in MLZ, partially and more slowly in KOH.

Specimen examined. Finland, Varsinais-Suomi, Parainen, Petteby, Stornäset (Paltbacken), in coniferous forest among mosses, 30 Sept. 1990, *T. Lindholm* (TUR 102134).

Notes — *Otidea papillata* is only known from two Finnish collections and its apothecial colours in fresh state are still unknown. It is a distinct species, characterised by cup-shaped apothecia with conspicuous warts on the outside, and small spores (Harmaja 1976). Two diagnostic characters have been observed in the two collections examined: 1) a very poorly differentiated ectal excipulum of *textura prismatica* to *textura intricata*, which is unique within the *Otidea* species studied by us; and 2) scattered brown resinous exudates on the hyphae of the medullary excipulum, that are somewhat reminiscent of those in *O. bufonia*. Harmaja (1976) emphasised the high warts on the outside of the apothecia as a unique character for *O. papillata*, but two additional *Otidea* species, *O. tuomikoskii* and *O. nannfeldtii*, have as high or higher warts. These two species have in fact been confused with *O. papillata* (Lundell et al. 1985, Van Vooren et al. 2008). *Otidea tuomikoskii* is distinguished from *O. papillata* by narrowly ear-shaped apothecia, a yellow reaction of the excipulum in KOH, an ectal excipulum of *textura angularis*, and by lacking pigmented exudates on the hyphae of the medullary excipulum. Highly warted apothecia of *O. nannfeldtii* probably resemble *O. papillata* more. However, *O. nannfeldtii* possesses pigmented resinous exudates at the septa in the medullary excipulum, resinous exudates of the ectal excipulum that convert into amber drops, and most importantly, an ectal excipulum of *textura angularis*.

Otidea leporina clade

Apothecia ear-shaped, yellowish ochre to brown. Resinous exudates on the ectal excipulum converting into reddish grey drops in KOH. Associated with conifers.

Species — *Otidea leporina*, *O. pseudoleporina*.

7. *Otidea leporina* (Batsch) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 330. 1870 ‘1869–1870’ — Fig. 4a, 10

Basionym. *Peziza leporina* Batsch, Elench. Fung. 1: 117. 1783: Fr., Syst. Mycol. 2: 47. 1822.

≡ *Scodellina leporina* (Batsch) Gray, Nat. Arr. Brit. Pl. 1: 668. 1821.

≡ *Helvella leporina* (Batsch) Franchi, L. Lami & M. Marchetti, Rivista Micol. 1: 63. 1999.

≡ *Helvella auricula* Schaeff., Fung. Bavar. Palat. Nasc. 4: 103. 1774 (‘*Elvela*’).

≡ *Wynnella auricula* (Schaeff.) Boud., Icon. Mycol. list prél. 600 sp.: (2). 1904.

≡ *Otidea auricula* (Schaeff.) Sacc., Syll. Fung. 8: 95. 1889.

Lectotype designated here: Schaeffer, Fung. Bavar. Palat. Nasc. 2: t. 156. 1763 (‘*Elvela decima tertia*’). *Epitype* designated here: Sweden, Jämtland, Östersund, Andersön Nature Reserve, under *Picea abies* on rich ground, 28 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.93 (S); MycoBank MBT178082.

= *Otidea leporina* f. *minor* Rehm, Ber. Naturhist. Vereins Augsburg 26: 63: 1881.

≡ *Otidea leporina* var. *minor* (Rehm) Sacc., Syll. Fung. 8: 94. 1889.

Lectotype designated here: Germany, Leipzig, in der Harth, in spruce forest, Aug. 1873, *G. Winter*, Rehm Ascomyceten no. 251 (S-F88382) ! *Isolectotype* (UPS F-641412) !; MycoBank MBT178088.

= *Otidea leporina* f. *major* Rehm, Hedwigia 3–4: 2. 1883.

= *Otidea leporina* var. *rubescens* Velen., Monograph. Discom. Bohemiae 1: 354. 1934.

Lectotype designated here: Czech Republic, Kosoř near Prague, Sept. 1920, *F. Fechtner* (PRM 614790) !; MycoBank MBT200087.

= *Otidea myosotis* Harmaja, Karstenia 15: 32. 1976.

Holotype. Finland, Etelä-Karjala, Hamina, Vehkalahti, Pyhältö, mixed forest, 3 Oct. 1970, *L. Fagerström* (H6003548) !

= *Otidea crassa* W.Y. Zhuang, Mycotaxon 94: 366. 2006 (‘2005’).

= *Otidea fuckelii* M. Carbone & Van Vooren, Rivista Micol. 52: 322. 2010 (‘2009’).

Holotype. Austria, Nassau, in pinetis umbrosis, Fungi Rhen. Exs. no. 1233 (G00110768). *Isotype* (S-F114092) !

Misapplied names

– Non *Wynnella auricula* sensu Boudier, Icon. Mycol. livr. 26: n°. 535, pl. 250. 1909 (preliminary text with ‘circulaires’) (= *Wynnella silvicola* (Beck) Nannf.).

Apothecia gregarious or caespitose, 17–52 mm high, 4–25 mm wide, narrowly to broadly ear-shaped, split, stipitate or sessile. *Hymenium* yellowish brown (5C6), cinnamon brown (5D6), pale ochre brown (5A5, 5B6) to orange brown (6C7, 6D6), sometimes dark brown (5D8, 5F8, 6E8) when young, seldom with pale pink stains (6A2), bruised margin orange brown (6D8), when dried cinnamon brown (5A5, 5B5) to rusty brown (6D7, 6D8). *Receptacle surface* ochre brown (5B6), hygrophanous, in drying paler ochre brown (4A4, 4A5, 4B6),

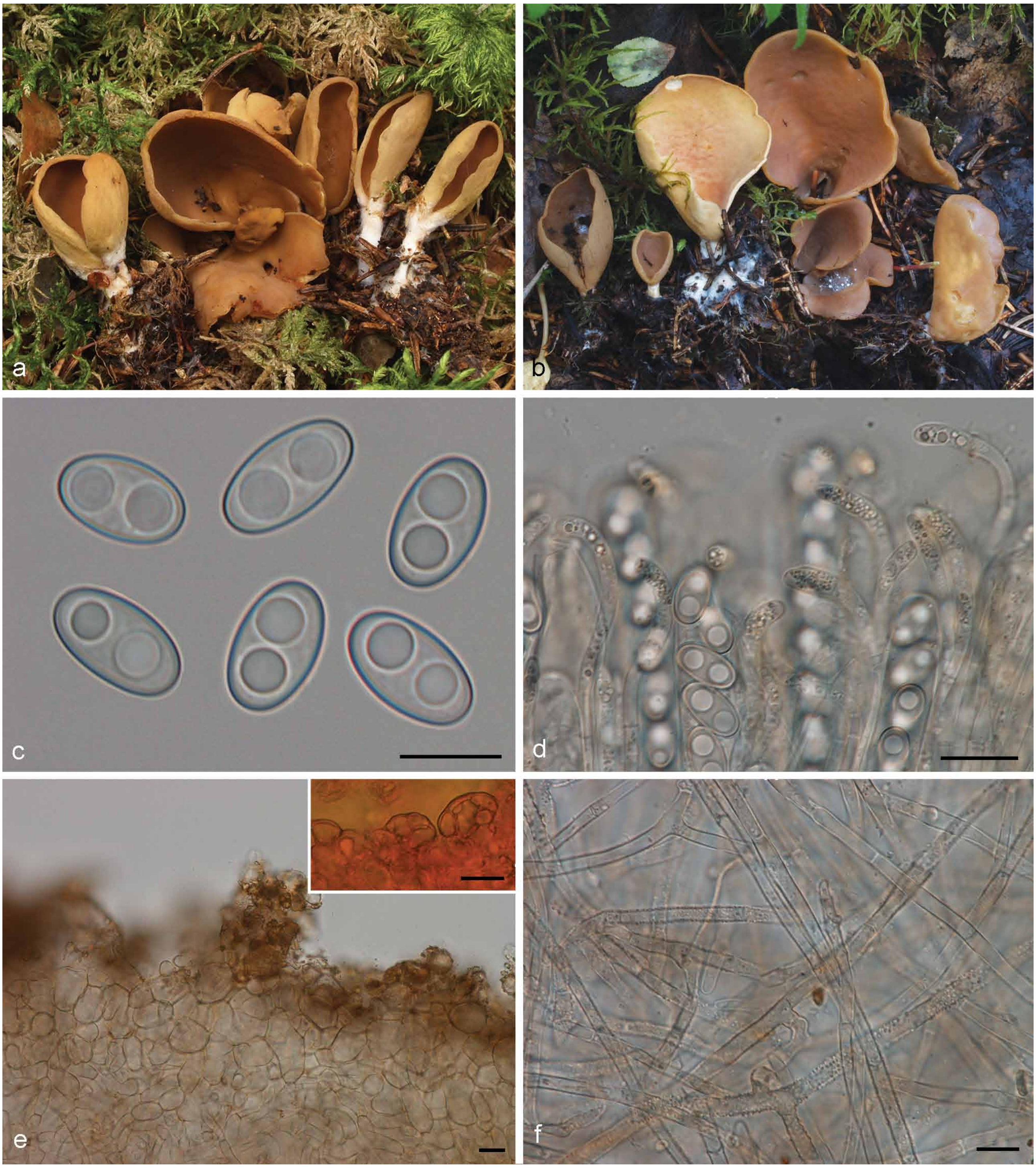

Fig. 10 *Otidea leporina**. a, b. Apothecia; c. spores; d. paraphyses; e. ectal excipulum with resinous exudates, insert shows close-up of amber drops on the ectal excipulum in Melzer's reagent; f. basal mycelium pale brown, with very small, regularly arranged, resinous exudates (a: KH.09.93, epitype; b: KH.09.102; c–g: KH.11.02). — Scale bars = 10 µm; * = all fresh material.

when dried yellowish brown (5C7, 5C8), furfuraceous to finely warty, seldom wrinkled at the base. Warts conical to flattened, gregarious, concolorous, sometimes darker than the background, golden brown. *Stipe* 4–15 × 2–8 mm. *Taste* slightly bitter. *Basal tomentum and mycelium* abundant, white to cream white (5A3), sometimes very pale brown when dried. *Spores* broadly ellipsoid, sometimes inequilateral, with two large guttules, smooth, hyaline, (12–)12.5–14(–15) × 7–8.5 µm (L_m = 12.8–13.8 µm, W_m = 7.5–8.2 µm, Q_m = 1.6–1.8; n = 16). *Paraphyses* curved to hooked, of the same width or slightly enlarged at apices, 2.5–4 µm wide, without notches or with 1–3 low notches, seldom forked at apices, when fresh containing small, refractive, light yellow guttules; when dried small, refractive, hyaline granules. *Asci* 170–215 × 9–10.5 µm. *Apothecial section* 700–900 µm thick. *Subhymenium* c. 80–100 µm thick, of dense *textura intricata*, visible as an orange-brown darker zone, cells cylindrical to swollen. *Medullary excipulum* of *textura intricata*, 300–550 µm thick, sometimes differentiated into two parts: a) *textura angularis* underneath the subhymenium, 40–50 µm thick, cells 6–12 µm broad; b) *textura intricata*, hyphae 5–13 µm wide, sometimes slightly swollen, thin-walled to slightly thick-walled, hyaline to very pale brown, sometimes with yellow-brown resinous exudates at septa. *Ectal excipulum* of *textura angularis*, 85–110 µm thick, cells thin-walled, pale brown, 15–48 × 12–31 µm. Surface with broadly conical warts, 50–85 µm high, formed by short, fasciculate, hyphoid hairs, of 2–4 subglobose to elongated cells, constricted at septa, 10–16 µm wide, sometimes with a gelatinous sheath. Resinous exudates abundant, yellow brown, sometimes dissolving in part into amber drops or converting into reddish particles in MLZ, dissolving into yellowish reddish grey heterogeneous drops in KOH. *Basal mycelium* of 3–4.5(–6) µm wide, hyaline to pale brown hyphae, unchanged in KOH, smooth or with very small, regularly arranged, spheroid, pale brown, resinous exudates, dissolving in MLZ, and partially in KOH.

Specimens examined. Canada, Québec, Le Verendrye Park, on ground under spruce, 16 Sept. 1965, *M.E. Elliot* 65-123 (UPS F-629640). – Czech Republic, Central Bohemian region, Zdice, Aug. 1924, *F. Fechtner* (PRM 614787, as *O. felina*); in piceto ad aciculos, Sept. 1925 (PRM 148836); Prague-West district, Kosoř near Prague, Sept. 1920, *J. Velenovský* (PRM 614792, as *O. umbrina*). – Denmark, Bornholm, Rø Plantage, coniferous forest, 29 Sept. 1985, *W. Rummel* (C-F-47633); N Jylland, Langdal Plantage (near Tranum), under *Juniperus*, near *Picea*, 13 Aug. 2009, *T. Læssøe*, TL-13769 (C); N Jylland, Rønhøj Plantage, 7 Oct. 1962, *A. Hauerbach* (C-F-86691); Jylland, Virklund, Silkeborg Sønderskov, in moss, coniferous forest, 26 Sept. 1964, *H. Dissing* (C-F-48298); Sjælland, Bromme Plantage, N of Sorø, under *Picea*, 9 Oct. 1965, *H. Dissing* (C-F-48299). – Finland, Etelä-Häme, Mustiala, in pineto, 29 Aug. 1866, *P.A. Karsten* (UPS F-146429); Perä-Pohjanmaa, Rovaniemi, Kaittiainen, acidic *Picea* forest, 11 Sept. 2011, *T. Kekki*, TK407 (TUR); Perä-Pohjanmaa, Rovaniemi, Pisajärvi, old *Picea* forest, 2 Sept. 2011, *T. Kekki*, TK304 (TUR); Perä-Pohjanmaa, Rovaniemi, Välljoki, calciferous *Picea* forest, 25 Aug. 2011, *T. Kekki*, TK231 (TUR). – France, Loire, La Chamba, au sol dans la litière d'aiguilles d'épicéa, 27 Sept. 2008, *N. Van Vooren*, NV 2008.09.28 (dupl. S). – Germany, Thüringen, in silvis abiegnis, *Kl. & Op.* (UPS F-629404, Klotzsch, Herb. Viv. Mycol. 143). – Norway, Nord-Trøndelag, Kvam, Noem Northeast, under *Picea*, among *Rhytidiadelphus squarrosus*, 2 Sept. 2009, *H. Lindström*, KH.09.131 (S); Nord-Trøndelag, Namdalseid, Flåbekkåsen Nature Reserve, *Picea* and *Pinus* old-growth forest, on acidic soil, among mosses, 4 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.141 (S); Nord-Trøndelag, Steinkjer, Skrattåsen, in rich *Picea abies* forest, 5 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.145 (S); ibid., KH.09.147 (S). – Sweden, Härjedalen, Torkilstöten, Ljungdalen, on an active anthill in *Picea* forest, 19 Aug. 2011, *J.C. Zamora & I. Olariaga*, KH.11.02 (S); Jämtland, in the surroundings of Sällsjö, in young stand of *Picea abies*, with *Betula* and *Salix*, 29 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.100 (S); ibid., KH.09.102 (S); Jämtland, SW of Mörsil, Sandtjärndalen Nature Reserve, under *Picea abies* on rich ground, 7 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.156 (S); Lappland, Ekopark Vuollerim, stream from Brännmyran, *Picea* forest, 28 Aug. 2008, *M. Karström*, MK0828 (S); Lappland, Jokkmokk, 'Nornaskogen' by Ållojaur, mossy *Picea* forest, on rich ground, 29 Aug. 2011, *K. Hansen & I. Olariaga*, KH.11.12 (S); ibid., KH.11.14 (S); Lappland, Jokkmokk, Ultevis Fjällurskog Nature Reserve, Sitoätno, near a *Picea*, 31 Aug. 2011, *K. Hansen & I. Olariaga*, KH.11.33 (S); ibid., KH.11.36 (S); Lappland, Kuouka, 15 km SE Messaure, herb-rich *Picea* forest on rich ground, among mosses, 3 Sept. 2011, *K. Hansen & I. Olariaga*, KH.11.67 (S); Lappland, S of Kvikkjobb-Kabla FUR Nature Reserve, by Kassavare Mt, Köpenhamn, under *Picea*, mossy place on acidic ground, 1 Sept. 2011, *K. Hansen & I. Olariaga*, KH.11.76 (S); Närke, Knista, Lekhyttan, Kungshall, under *Picea* on calcareous ground, among mosses and litter, 12 Sept. 2008, *J. Santos*, JS.08.065 (S); ibid., coniferous forest, with old *Picea* and *Pinus*, *K. Hansen*, KH.08.108 (S); Skåne, Loshult, Lilla Loshult, *Picea* forest, 5 Sept. 1998, *S.-Å. Hanson*, SÅH 105838 (C); Uppland, Stockholm, Enebyberg, Rinkebyskogen, under *Picea* and *Betula* on acidic ground, 2 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.169 (S); Uppland, Täby, Rönninge, close to parking place by Arninge, under *Picea* on thick litter layer, 21 Sept. 2008, *J. Santos*, JS.08.92 (S); Uppland, Uppsala, Ersta Nature Reserve, on soil under *Picea* in young plantation, 23 Sept. 2008, *J. Santos & K. Hansen*, JS.08.99 (S); Uppland, Uppsala, Sävja, Norra Lunsen Nature Reserve, under *Picea*, 28 Aug. 2008, *J. Santos*, JS.08.46 (S); Värmland, Gustav Adolf, Hagfors, Malmbackarna, on moss, under *Picea* and *Betula*, 10 Aug. 2009, *F. Turander* s.n. (S). – USA, California, Del Norte Co., Lake Earl Wildlife Area, 14 Dec. 1997, *E.T. Peterson* (OSC 56824); ibid., 15 Dec. 1997 (OSC 56825); ibid., under *Picea sitchensis*, *Pinus contorta*, *Abies concolor*, 26 Nov. 2001, *M. Castellano & E. Cazares* (OSC 108820); California, Humboldt Co., Big Lagoon Park, 14 Dec. 1956, *A.H. Smith* 56668 (UPS F-629302); ibid., under *Picea*, 16 Dec. 1956, *A.H. Smith* 56799 (UPS F-629304); ibid., 23 Dec. 1956, *A.H. Smith* 56954 (UPS F-629305); Colorado, Tolland, on ground in coniferous woods, 28 Aug. 1920, *F.B. Cotner* (UPS F-629390); Oregon, Lincoln Co., Fogarty Creek State Park, 15 Oct. 1997, *E.T. Peterson* (OSC 56784); Washington, Okanogan National Forest, Pasayten Wilderness, under *Picea engelmannii*, *Pseudotsuga menziesii*, *Abies lasiocarpa*, *Pinus contorta*, 16 Sept. 1999, *R. Davis* (OSC 108856).

Notes — *Otidea leporina* is probably the most common *Otidea* species in boreal coniferous forests of Europe. In the Alps it often occurs together with *Cudonia circinans*, an association not seen in Fennoscandia. It is characterised by ear-shaped, brown apothecia, together with relatively broad spores that are almost unique within *Otidea*. *Otidea brunneoparva* shares similar spores, but differs from *O. leporina* in the darker brown apothecia and strongly notched paraphyses. Other species of *Otidea* that macroscopically resemble *O. leporina* are distinguished by different spore size and shape.

Our morphological and molecular study of the holotype of *O. myosotis* shows it is a synonym of *O. leporina* (Hansen & Olariaga 2015). The original description of *O. myosotis* (Harmaja 1976) pointed out the apothecial shape and colours, and paraphyses as diagnostic characters, all of which agree with our concept of *O. leporina*. Recently, Harmaja (2009a) stated that the excipular resinous exudates in *O. leporina* convert in MLZ into reddish particles and show no reaction in *O. myosotis*. In the material of *O. leporina* examined by us, the resinous exudates dissolve in part, can appear unchanged or can convert into reddish particles. Sometimes, small amber-drops have also been observed, though not as strikingly as in other species. Therefore, it seems that the reaction of the exudates in MLZ is variable within *O. leporina*, and cannot be used to separate *O. myosotis* from *O. leporina*. *Otidea crassa* is a synonym based primarily on the GenBank LSU sequence of the type collection (DQ443444).

Nomenclatural notes — When Batsch (1783) described *Peziza leporina*, he referred to Schaeffer's plate (1763), being unaware or disregarding Schaeffer's later description of '*Elvela' auricula* Schaeff. (1774) based on the same plate. Since Fries (1822) sanctioned Batsch's name, referring to *H. auricula* Schaeff. (as *P. auricula* Schaeff.) as a synonym, *P. leporina* has priority. While most authors have interpreted the plate by Schaeffer (1763, t. 156) as a species that belongs to *Otidea* (e.g. Fuckel 1870, Rehm 1883, Bresadola 1898, Seaver 1904), others have considered it to represent the monotypic *Wynnella* (Gonnermann & Rabenhorst 1869, Quélet 1886). Recently, Franchi et al. (1999) stated that the Schaeffer plate represents *W. silvicola* and as they consider *Wynnella* to be part of the genus *Helvella*, they made the combination *Helvella leporina*. Carbone & Van Vooren (2010) expressed doubts about how to interpret the protologue by Batsch (1783) and Schaeffer's plate, and concluded the name is ambiguous and recommended it not be used. Instead they introduced the new name *O. fuckelii* for the *Otidea* species treated here. Based on our phylogenetic and morphological studies (see also Hansen & Olariaga 2015) this new name is, however, superfluous, since *O. myosotis* and *O. crassa* are shown to be synonyms of *O. leporina*.

The original Schaeffer plate shows several, more or less evenly coloured, light ochraceous brown apothecia, conforming to *O. leporina*, and not bi-coloured apothecia (dark reddish brown with a white base) as in *W. silvicola*. In our opinion, it leaves little doubt it shows a species of *Otidea*. To settle the use of the name *O. leporina*, and at the same time preserve the use of the well-established name, *W. silvicola* (Beck) Nannf. (Nannfeldt 1966), we propose a modern epitype for *Peziza leporina* Batsch: Fr. (Fig. 10a), which represents the *Otidea* species for which the name has most often been used. The epitype is from Sweden where Fries saw and studied living material, as indicated by the abbreviation '*v. v.*' (*vidi vivam*, seen living).

8. ***Otidea pseudoleporina*** Olariaga & K. Hansen, *sp. nov*. — MycoBank MB808972; ITS barcode GenBank: KM010112; Fig. 5e, 11

Etymology. From ancient Greek ψευδο-, which means 'false, fake', referring to a close relationship with *O. leporina*.

Holotype. USA, Oregon, Douglas Co., E of Mill Creek, under *Pseudotsuga menziesii*, *Abies concolor*, *Pinus lambertiana*, 19 Oct. 2010, *R. Helliwell*, rh101910 (OSC).

Misapplied names
– *Otidea cantharella* var. *minor* sensu Kanouse, Mycologia 41: 667. 1949.

Apothecia gregarious, 10–30(–50) mm high, 8–22(–31) mm wide, initially narrowly to broadly ear-shaped, margin rounded, then expanding and sometimes becoming irregularly cup-shaped, split, stipitate or sessile. *Hymenium* ochre-orange (4A6, 5A7) to pinkish orange (5A6, 5A7), sometimes with pink spots or stains (6A4), when dried orange-ochre (5A5, 5B5) to reddish brown (6D7). *Receptacle surface* ochre-brown (5B5), hygrophanous, in drying yellowish ochre (4A4, 4A5), when dried yellowish ochre (5A5) to brownish ochre (5B5), furfuraceous to finely warty, sometimes wrinkled at the base. Warts conical to rounded, gregarious, concolorous, sometimes distinctly darker than the background, reddish brown. *Stipe* 4–11 × 3–5 mm. *Basal tomentum and mycelium* abundant, white to pale yellow (4A2) or ochre (5A2). *Spores* ellipsoid, sometimes slightly inequilateral, with two large guttules, sometimes with up to 4 smaller guttules, smooth, hyaline, (9.5–)10–12(–12.5) × 5.5–6.5 µm (L_m = 10.2–11.6 µm, W_m = 5.7–6.4 µm, Q_m = 1.7–1.9; n = 6).

Fig. 11 *Otidea pseudoleporina*. a, b. Apothecia; c. apothecia†; d. spores in water†; e. paraphyses in water†; f. ectal excipulum in water† (a, d–f: rh101910, holotype; b, c: Moorefun 14). — Scale bars = 10 µm; † = dried material. — Photos: a. R. Helliwell; b. c. J. Moore.

Paraphyses curved to hooked, of the same width or slightly enlarged at apices, 2.5–4.5 µm wide, sometimes with 1–3 notches, apices seldom forked and rarely covered with a hyaline coating, when dried containing small, refractive, yellow granules. *Asci* 155–231 × 9–10 µm. *Apothecial section* 900–1200 µm thick. *Subhymenium* c. 80–100 µm thick, of dense *textura intricata*, visible as an orange-brown darker zone, of cylindrical to swollen cells. *Medullary excipulum* 500–750 µm thick, differentiated into two parts: a) *textura angularis* underneath the subhymenium, 150–200 µm thick, hyphae 8–18 µm broad; b) *textura intricata*, hyphae 5–10(–18) µm wide, sometimes slightly swollen, thin-walled to slightly thick-walled, very pale yellow, sometimes with yellow-brown resinous exudates at septa. *Ectal excipulum* of *textura angularis*, sometimes of a *textura prismatica*, 80–110(–150) µm thick, cells thin-walled to slightly thick-walled, pale yellow-brown, 13–37 × 8–27 µm. Surface with broadly conical warts, 77–115 µm high, formed by short, fasciculate, hyphoid hairs, of 2–3 subglobose to elongated cells, constricted at septa, 6–12 µm wide, sometimes with a gelatinous sheath. Resinous exudates abundant, yellow-brown, dissolving into amber drops in MLZ, partially to entirely dissolving into reddish grey heterogeneous drops in KOH. *Basal mycelium* of 3–5 µm wide, very pale yellow hyphae, unchanged in KOH, with very small, yellow resinous exudates, regularly arranged, spheroid, dissolving in MLZ, partially and more slowly dissolving in KOH.

Specimens examined. USA, California, Trinidad, under spruce, 30 Nov. 1956, *A.H. Smith* 56168 (UPS F-629690); Idaho, Idaho Co., Rickliff Creek Public Camp, on the ground in *Thuja-Tsuga* woods, 10 Oct. 1947, *W.B. Cooke* 21227 (UPS F-629388); Idaho, Papoose Creek, Seven Devils Mts, on the ground in Douglas fir association, 3 Sept. 1954, *A.H. Smith & H.E. Bigelow*, 47346 (UPS F-629331); Oregon, Bear Springs, Mt Hood National Forest, 18 Oct. 1947, *A.H. Smith* 27946 (UPS F-629430); Oregon, Benton Co., Corvallis, west side of NW Beechwood Place, scattered to clustered on rotting bark mulch and in thin grass under *Pseudotsuga menziesii*, 14 Nov. 2010, *N.S. Weber*, NSW 10202 (OSC 150347); ibid., 17 Nov. 2010, *N.S. Weber*, NSW 10200 (OSC 150345); ibid., 27 Nov. 2010, NSW 10201 (OSC 150346); Oregon, Douglas Co., E of Mill Creek, under *Pseudotsuga menziesii*, *Abies concolor*, *Pinus lambertiana*, 22 Oct. 2010, *J. Moore*, Moorefun 24 (OSC); Oregon, Douglas Co., Mill Creek, under conifers, 19 Oct. 2010, *J. Moore*, Moorefun 14 (S); Oregon, Douglas Co., Roseburg District Bureau of Land Management, under *Pseudotsuga menziesii*, *Arbutus menziesii*, *Castanopsis chrysophylla*, 11 May 1997, *J. Klein* (OSC 66261); Oregon, Douglas Co., south of Lemolo Lake, under conifers, 5 Nov. 2010, *R. Heliwell*, rh 179 (S); Oregon, Douglas Co., Thorn Unit I, under *Pseudotsuga menziesii*, *Tsuga heterophylla*, 21 Oct. 2010, *C. Durbecq*, Durbecq 16 (OSC); Oregon, Jackson Co., Medford Bureau of Land Management, Ashland Resource Area, Beaver Creek, under *Pseudotsuga menziesii*, *Arbutus menziesii*, *Toxicodendron diversilobum*, *Berberis piperiana*, 18 Dec. 2000, *R. Brock* (OSC 119311); Oregon, Jackson Co., Medford District Bureau of Land Management, Butte Falls Resource Area, under *Pseudotsuga menziesii*, *Calocedrus decurrens*, *Pinus lambertiana*, *Pinus ponderosa*, *Quercus kellogii*, *Rhus diversiloba*, *Berberis piperiana*, *Fragaria vesca*, *Moehringia macrophylla*, grasses, 8 Mar. 2000, *M. Wineteer* (OSC 72956); Oregon, Lane Co., Willamette National Forest, Blue River Ranger District, under *Pseudotsuga menziesii*, 18 Nov. 1999 (OSC 72296); Oregon, Marion Co., Breitenbuch Hot Springs Community, near Detroit Reservoir, in woods, 8 Nov. 1997, *J.W. Spatafora* (OSC 56809); Oregon, Mt Hood, among moss under conifers, 15 Oct. 1922, *L.E. Wehmeyer* (UPS F-629375); Oregon, Warm Springs R., Mt Hood National Forest, Skyline Trail, 29 Sept. 1947, *A.H. Smith & W.B. Gruber*, 27064 (UPS F-629689); Washington, Clallam Co., Olympic National Park, Whiskey Bend trailhead, 26 Nov. 1996, *E.T. Peterson* (OSC 56760); Washington, Fish Creek Region, Mt Rainier National Park, 25 Aug. 1948, *E.G. Simmons* 2067 (UPS F-629332); Washington, lower slopes of Rampart Ridge, W. of Longmire, Mt Rainier National Park, 4 Sept. 1948, *E.G. Simmons* 2172 (UPS F-629386); Washington, Park Creek, Mt Baker National Forest, 9 Sept. 1941, *A.H. Smith* 16755 (UPS F-629820); Washington, Pierce Co., Mt Rainier National Park, Lower Tahoma Creek, 29 Oct. 1996, *E.T. Peterson* (OSC 56749).

Notes — *Otidea pseudoleporina* is recognised by the broadly ear-shaped apothecia, ochre-orange to pinkish orange hymenium and small spores. Our multi-gene phylogenetic analyses (Hansen & Olariaga 2015) suggest *O. pseudoleporina* is the sister species of *O. leporina*. They share ear-shaped apothecia and resinous exudates on the outer excipulum that partly convert into heterogeneous reddish drops in KOH. *Otidea leporina* differs in the brown apothecia and larger, broadly ellipsoid spores. *Otidea pseudoleporina* resembles *O. nannfeldtii* and *O. formicarum* in the general apothecial shape and small spores. *Otidea nannfeldtii* is distinguished by most often lacking orange tones, having narrowly ear-shaped young apothecia, and ectal excipular resinous exudates turning reddish brown in KOH. *Otidea formicarum* is distinguished by having apothecia devoid of orange tones, and spores with a lower Q_m (1.6–1.7) than *O. pseudoleporina* (1.7–1.9).

The material cited by Kanouse (1949) under *O. cantharella* var. *minor* most likely represents *O. pseudoleporina*. *Otidea cantharella* var. *minor* as described by Boudier (1909a) has a pale ochre or grey hymenium, citrine yellow outside, and veins at the apothecial base, and represents a different species (see under *O. minor*). Peterson (1998) treated under *O. concinna* material that we refer to *O. pseudoleporina* and stated that Harmaja (1974) used the name *O. cantharella* for the same species. *Otidea concinna* is a well-known species in Europe, clearly distinct from *O. pseudoleporina* (see *O. concinna*). As for the name *O. cantharella*, the protologue describes a fungus with the colour of *Cantharellus cibarius* (Fries 1822), and we typify it with material of the large-spored species sometimes called *O. caligata* (see *O. cantharella*). So far *O. pseudoleporina* is only known from Western North America.

Otidea tuomikoskii clade

Apothecia ear-shaped. Receptacle surface with warts often more than 100 µm high. Basal tomentum light ochre to orange ochre. Spores small, 10–11 µm long. Sections of apothecia turning yellow in KOH, especially the subhymenium and ectal excipulum. Associated with conifers.

Species — *Otidea tuomikoskii*.

9. *Otidea tuomikoskii* Harmaja, Karstenia 15: 30. 1976 — Fig. 12

Holotype. Finland, Etelä-Häme, Lammi, Pappilankylä, Koiransuolenoja, in needles of *Picea abies* on an anthill, 9 Sept. 1972, *R. Tuomikoski* (H6002901) !

= *Otidea papillata* f. *pallidefurfuracea* Van Vooren & Hairaud, Bull. Mycol. Bot. Dauphiné-Savoie 188: 56. 2008.

Holotype. France, Jura, Les Rousses, tourbière près du lac des Rousses, au sol dans la litière d'aiguilles, sous épicéas (*Picea abies*), 19 Sept. 2007, *N. Van Vooren*, NV 2007.09.27 (PC). *Isotype* (S) !

Misapplied names

– *Otidea papillata* sensu Lundell, Nannfeldt & Holm, Fungi Exs. Suec. 66: 3282. 1985.

Apothecia gregarious to caespitose, 17–60 mm high, 7–30 mm wide, long and narrowly ear-shaped, split, stipitate or sessile. *Hymenium* pale whitish ochre (4A2, 4A3) to ochre yellow (4A4–4A6) rarely with pink stains, when dried light ochre yellow (4A4) to ochre (5B7, 5B8). *Receptacle surface* brownish ochre (4B7, 4C7) to yellow brown (5B6–5D6), hygrophanous, ochre yellow (4A5, 4A6, 4B6) in drying, when dried yellowish brown (5C8, 5D8), warty, rarely wrinkled at the base. Warts conical, gregarious, brown, distinctly darker than the background or rarely lighter. *Stipe* 3–6 × 2–3 mm. Smell faintly aromatic. *Basal tomentum and mycelium* abundant, light ochre (5A2) to orange-ochre (5A4). *Spores* ellipsoid, slightly inequilateral, with two large guttules, and sometimes with 1–4 smaller granules, smooth, hyaline, (9.5–)10–11(–12) × 5.5–6.5(–7) µm (L_m = 10.3–11.4 µm, W_m = (5–)5.5–6.5(–7.5) µm, Q_m = 1.7–1.9; n = 15). *Paraphyses* curved to hooked, often broader at apices, 2.5–5(–6) µm wide, sometimes with up to two shallow notches or forked at

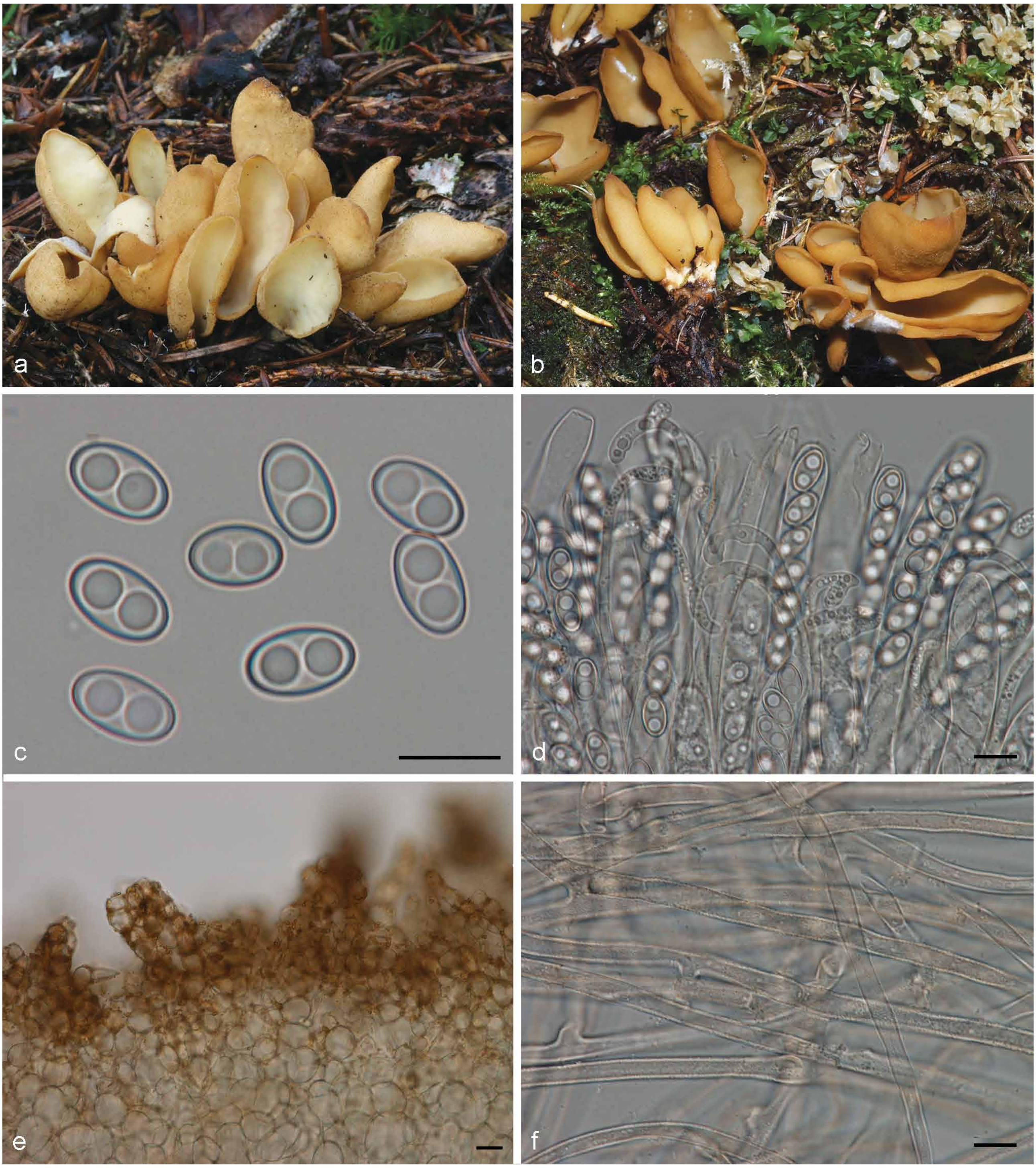

Fig. 12 *Otidea tuomikoskii**. a, b. Apothecia; c. spores; d. paraphyses; e. ectal excipulum; f. basal mycelium (a: JS.08.68; b–f: KH.11.77). — Scale bars = 10 µm; * = all fresh material. — Photos: a. J. Santos.

apices, when fresh containing small to large, refractive, hyaline to pale yellow guttules; when dried pale yellow. *Asci* 113–199 × 9–11.5 µm. *Apothecial section* 600–700(–1200) µm thick, pale to bright yellow in KOH. *Subhymenium* c. 50–90 µm thick, of dense *textura intricata*, visible as a yellowish brown zone. *Medullary excipulum* of *textura intricata*, 300–500(–850) µm thick, hyphae 3–13 µm wide, thin-walled to slightly thick-walled, hyaline to very pale yellow, without resinous exudates at septa. *Ectal excipulum* of *textura angularis*, 80–120 µm, cells thin-walled, hyaline to light yellow, 13–40 × 8–25 µm. Surface with conical warts, 55–177 µm high, formed by fasciculate, short, hyphoid hairs, of 3–8 globose to elongated cells, constricted at septa, 7–15 µm wide, sometimes with a gelatinous sheath. Resinous exudates abundant, yellow-orange to yellowish brown, dissolving into amber drops in MLZ, unchanged in KOH. *Basal mycelium* of 3.5–6(–7.5) µm wide, often thick-walled, septate, hyaline to very pale yellow hyphae, unchanged in KOH, with regularly arranged, spheroid, yellow to orange resinous exudates, dissolving in MLZ, partially and more slowly in KOH.

Specimens examined. Denmark, NW Jylland, Klim Bjerg, soil along forest road, *S.A. Elborne & K. Hansen*, 16 Sept. 1998, KH.98.92 (C-F-53155). – Estonia, Põlvamaa, ad terram in piceto humida, 11 Aug. 1960, *A. Elango* (UPS F-629392). – Finland, Perä-Pohjanmaa, Rovaniemi, Pisajärvi, old *Picea* forest, 2 Sept. 2011, *T. Kekki*, TK305 (TUR). – France, Charente-Maritime, île de Ré, près du camping ‘La Bonne Étoile’, under *Pinus maritima* and *Quercus ilex*, on leaf litter, 26 Nov. 2006, *M. Hairaud*, NV 2006.11.05 (dupl. S); Rhône, Les Halles, col de Croix-Régis, 25 Oct. 2006, *J. Cavet*, NV 2006.10.33 (dupl. S); Rhône, Saint-Nizier-d’Azergues, forêt de Pramenoux, sous *Picea abies*, 20 Sept. 2008, *N. Van Vooren*, NV 2008.09.08 (dupl. S). – Germany, Lower

Saxony, Lüneburg, Boitze, *Pinus* and *Abies*, Oct. 2010, *M. Vega* private herb. s.n. (dupl. S-F256977). – Norway, Nord-Trøndelag, Snåsa, Bergsåsen Nature Reserve, under *Picea* and *Pinus*, 2 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.130 (S). – Spain, Navarre, Orokieta, Loiandi, *Picea abies* plantation, 17 Oct. 2008, *J.M. Lekuona* (ARAN-Fungi A5041195). – Sweden, Lappland, 3 miles NW Vuollerim, Bombmurkleskogen, along the Stora Luleälven, herb-rich *Picea* forest, 19 Aug. 2000, *M. Karström*, MK200065 (S); Lappland, Norrbotten, Messaure, Kaltisbäcken Nature Reserve, herb rich *Picea* forest, 3 Sept. 2011, *M. Karström*, KH.11.60 (S); Medelpad, Södra Sillre, Hussborg, on wood, 22 Aug. 1998, *K. Olofsson* (S-F256896); Närke, Hidinge, Lekhyttan, Katte Majaskogen, coniferous forest on lime rich soil, *B. Wasstorp*, 13 Sept. 2008, JS.08.77 (S); Närke, Snavlunda, Ö Snavlunda Nature Reserve, under *Picea* in a mixed forest, 12 Sept. 2008, *L.G. Hellsten & A. Stridvall*, JS.08.68 (S); Närke, Vintrosa, Kanterboda skans Nature Reserve, on soil under conifers, 10 Sept. 2008, *A.B. Nilsson*, JS.08.60 (S); Skåne, Loshult, Lilla Loshult, *Picea* forest with a few broadleaf trees (*Betula*, *Quercus*), 5 Sept. 1998, *S.-Å. Hanson*, SÅH 105768 (C); Södermanland, Nacka, Kvarnhagen by Söderbysjön, on soil in shadow, moist area, under *Picea*, 26 Sept. 2008, *J. Santos*, JS.08.100 (S); Uppland, Björklinge, Drälinge, amongst needles and mosses under pine in coniferous woods, 10 Sept. 1936, *H.G. Bruun & H. Smith* (S-F92983, Fungi Exs. Suec. 3282); Uppland, Trehörningsskogen Nature Reserve, under *Picea* on rich ground, on needle litter and decayed wood, 1 Sept. 2011, *M. Prieto & I. Olariaga*, KH.11.77 (S). – USA, California, Del Norte Co., Earl Lake State Park, access by Sand Hill Road, 15 Dec. 1997, *M. Madsen & R. Davis* (OSC 56826); California, Humboldt Co., Trinidad, Nov. 1931, *H.E. Parks* 3749 (UPS F-629376); Oregon, Benton Co., Corvallis, McDonald-Dunn Research Forest, under conifers, 23 Oct. 1996, *E.T. Peterson* (OSC 56761); Oregon, Benton Co., Corvallis, west side of NW Beechwood Place, scattered clusters of apothecia on duff and adjacent to rotting wood under *Pseudotsuga menziesii*, 19 Nov. 1997, *N.S. Weber*, NSW 8553 (OSC 150344); Oregon, Douglas Co., Bureau of Land Management, Roseburg District, Swiftwater Resource Area, under *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Polystichum munitum*, *Berberis nervosa* and *Holodiscus tricolor*, 8 Nov. 2000, *R. Furriel* (OSC 105550); Oregon, Marion Co., Salem District Bureau of Land Management, Cascades Resource Area, under *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Gautheria shallon*, *Polystichum munitum*, *Berberis nervosa*, *Oxalis oregana*, *Acer circinatum*, *Alnus rubra* and *Rhododendron macrophyllum*, 12 Nov. 1997, *K. Dougan* (OSC 66350); Washington, Bremerton, 26 Oct. 1942, *J.B. Flett* (UPS F-629383); Washington, Eatonville, 18 Oct. 1954, *A.H. Smith* 49143 (UPS F-629385); Washington, Lower Nisqually R., Mt Rainier National Park, 2 Sept. 1948, *A.H. Smith* 30888 (UPS F-629384).

Notes — *Otidea tuomikoskii* is characterised by the narrowly ear-shaped apothecia, with high warts on the outside, small spores, and the excipulum almost always turning yellow in KOH, together with the ochre to orange-ochre basal tomentum in dried specimens. *Otidea nannfeldtii* is probably the species that resembles *O. tuomikoskii* most, but *O. nannfeldtii* has lower warts, lacks orange tones in the basal tomentum, has paraphyses only rarely with slightly swollen areas, and resinous exudates on the outer excipulum that turn reddish in KOH. *Otidea papillata* shares with *O. tuomikoskii* conspicuous dark warts on the outside of the apothecia (see under *O. papillata*).

The yellow KOH reaction of the excipulum, especially strong in the subhymenium and ectal excipulum, has been observed to be constant, although weak in some collections. The KOH reaction is stronger in recent collections, and can also be macroscopically observed in fresh apothecia. The holotype of *O. tuomikoskii* is from an anthill (Harmaja 1976), but *O. tuomikoskii* most often produces apothecia among needle litter or even on very decayed wood, in coniferous forests. It is widespread in Europe, where it occurs in coniferous plantations, and in Western North America (Peterson 1998), and has been found in Asia (Cao et al. 1990).

Otidea cantharella clade

Apothecia ear-shaped, or cup-shaped and entire, usually clearly stipitate. Spores exceeding 20 µm, biguttulate and with several additional small guttules (except in *O. brunneoparva*). Paraphyses often strongly notched. Associated with *Picea*.

Species — *Otidea brunneoparva*, *O. cantharella*, *O. propinquata*.

10. *Otidea brunneoparva* K. Hansen, M. Carbone, Olariaga & Van Vooren, *sp. nov.* — MycoBank MB537590; ITS barcode GenBank: KM010026; Fig. 13, 14

Etymology. Harmaja (2009a) used the epithet *brunneoparva* to provisionally name this species. The name is validated here and refers to the small size and brown colour of the apothecia.

Holotype. Sweden, Närke, Knista, Lekhyttan, Kungshall, calcareous old-growth forest, in thick litter layer, with *Picea* and *Pinus*, 12 Sept. 2008, *K. Hansen*, KH.08.107 (S). *Isotype* (C).

Apothecia gregarious, 12–35 mm high, 7–25 mm wide, initially ear-shaped, apex subacute, broadly ear-shaped in the end, seldom almost cup-shaped, split, stipitate. *Hymenium* dark brown (6F3–6F7), sometimes olivaceous brown (5D7, 5E7, 5E8) or reddish brown (7F3–7F5), sometimes paler in the margin, purplish ochre (5B3, 5B4, 6D7), when dried olivaceous brown (5F4, 5F5, 5F7, 5E7) or dark brown (6E6, 7F7, 7F8). *Receptacle surface* concolorous or slightly lighter, dark brown (5F6, 6F7, 7F8), slightly hygrophanous, in drying golden brown (5D6, 5D7), when dried dark brown (6E7, 7E7) to cinnamon brown (5D7, 6D7, 6E7), furfuraceous, sometimes finely warty at the base, often longitudinally wrinkled at the base, sometimes almost reaching the margin. Warts hemispherical, gregarious, concolorous, sometimes darker or paler brown than the background. *Stipe* 4–7 × 2–3 mm. *Basal tomentum and mycelium* white to very pale brown, when dried ochre brown. *Spores* ellipsoid to broadly ellipsoid, sometimes very slightly inequilateral, with two large guttules, seldom with 1–2 additional smaller granules, smooth, hyaline, (11–)11.5–14(–15) × 6.5–8.5 µm (L_m = 11.7–13.8 µm, W_m = 7.1–8.3 µm, Q_m = 1.6–1.7; n = 6). *Paraphyses* hooked, often inrolled, of the same width or slightly enlarged at the apices to 3–5.5 µm wide, often with clear notches or forked at apices, when fresh containing refractive, pale yellowish brown guttules, restricted to the uppermost part of the paraphyses; when dried pale yellow. *Asci* 131–195 × 8–10 µm. *Apothecial section* 700–800 µm thick. *Subhymenium* c. 100–120 µm thick, visible as a darker brown zone, cells cylindrical to swollen, densely arranged, with scattered brown resinous exudates at septa. *Medullary excipulum* of loosely woven *textura intricata*, 300–500 µm thick, hyphae cylindrical to slightly swollen, thick-walled, 5–11 µm wide, hyaline to very pale brown, sometimes with brown resinous exudates at septa. *Ectal excipulum* of *textura angularis*, 80–100 µm, cells thick-walled, yellowish brown, 20–47 × 12–25 µm. Surface with broadly conical warts, 25–65 µm high, composed of fasciculate, short hyphoid hairs. Non-warted parts with scattered hyphoid hairs, of 2–3 subglobose to elongated cells, 7.5–10.5 µm wide, slightly constricted at septa, sometimes with a thin gelatinous sheath. Resinous exudates abundant, yellowish to reddish brown, dissolving into amber drops in MLZ. *Basal mycelium* of 3–4.5 µm wide, very pale brown hyphae, unchanged in KOH, smooth or with very small, resinous exudates, dissolving in MLZ.

Specimens examined. Finland, Etelä-Häme, Hämeen, Lammi, Evo, Kotinen virgin forest, mesic forest of the *Myrtillus* type, in needle litter of *Pinus sylvestris* and *Picea abies* in basal part of an active anthill, 8 Sept. 1978, *H. Harmaja* (S-F249386); Kainuu, Paltamo, Saukkovaara, under *Picea abies* in moist spring-fed site, nearly in water, 24 Aug. 2011, *M. Lahti* (TUR-A 198582); Koillismaa, Kuusamo, Oulanka National Park, first part of the Kiutaköngäs trail, on rich soil among *Picea* and *Betula* leaves, 25 Aug. 2008, *M. Carbone* (TUR-A 198581); ibid., 16 Aug. 2009 (S-F257086, dupl. TUR-A 198579); ibid., 14 Aug. 2010 (TUR-A 198580). – Sweden, Jämtland, Östersund, Ändsjön Nature Reserve, on an abandoned anthill in rich *Picea* forest, 26 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.82 (S); Närke, Hidinge, Lekhyttan, Katte Majaskogen, coniferous lime-rich forest, in litter, 13 Sept. 2008, *B. Wasstorp*, JS.08.73 (S); Närke, Knista, Lekhyttan, Kungshall, calcareous oldgrowth forest, in thick litter layer, with *Picea* and *Pinus*, 12 Sept. 2008, *J. Santos*, JS.08.66 (S); ibid., JS.08.69 (S).

Notes — *Otidea brunneoparva* is morphologically and genetically a clearly distinct species. It is macroscopically character-

Fig. 13 *Otidea brunneoparva* apothecia. a. KH.08.107, holotype; b. JS.08.66; c. TUR-A 198579; d. TUR-A 198580. — Photos: b. J. Santos; c, d. M. Carbone.

ised by stipitate, broadly ear-shaped apothecia with dark brown colours and sometimes olivaceous shades. Microscopically, the spore shape and size are diagnostic (Fig. 14a), although with wide variation. The strongly inrolled and notched apices of the paraphyses are very characteristic (Fig. 14b) and otherwise only found in a few species like *O. propinquata* or *O. daliensis.* The thick-walled, yellowish brown, angular cells forming the outer excipulum are diagnostic too (Fig. 14c, d); such thick-walled cells in the outer excipulum are only otherwise found in *O. propinquata*. The six ITS sequences of *O. brunneoparva*, from five different localities in Finland and Sweden, are identical or with 3–8 bp differences. The ITS nucleotide diversity within *O. brunneoparva*, as sampled here, is 0.74 % per site. Phylogenetic analyses of four gene-regions (Hansen & Olariaga 2015) show *O. brunneoparva* forms a distinct monophyletic group with *O. propinquata* and *O. cantharella*. These three species are nevertheless, easily distinguished both macro- and microscopically.

The distinctive spores of *O. brunneoparva* are only otherwise found in *O. leporina* within *Otidea*. *Otidea brunneoparva* is clearly distinguished from *O. leporina* by the darker coloured apothecia and notched paraphyses. *Otidea bufonia*, *O. mirabilis* and *O. smithii* share dark brown colours with O. *brunneoparva*, but clearly differ in apothecial shape and stature (*O. brunneoparva* being more delicate), narrower spores (L_m = 6.3–7.3 µm, Q_m = 1.9–2.5) of different shape (fusoid in *O. bufonia* and *O. mirabilis*) and the resinous exudates on the ectal excipulum not dissolving into amber drops. *Otidea fusconigra* was published as a provisional name too. It also resembles *O. brunneoparva* in the dark brown apothecia, and spore size and shape (Jamoni 2004). Nevertheless, the paler hymenium colour (‘grey caffelatte’), the paraphyses without notches and the habitat among alpine dwarf *Salix*, suggests *O. fusconigra* is a different species. ITS and LSU sequences of *O. fusconigra* (collection GMFN 2293), obtained by us, confirms *O. fusconigra* is not conspecific, but a sister taxon to *O. smithii*.

Following Cao et al. (1990), *O. brunneoparva* keys out as *O. olivacea* J.Z. Cao & L. Fan. The cup-shaped, dark brown apothecia, with olivaceous tinge, suggest these may be closely related. However, the spores of *O. olivacea* were described as considerably longer (14–17 × 8–8.5 µm), almost non-overlapping with those of *O. brunneoparva*. Unfortunately, we were not able to get the type specimen of *O. olivacea* on loan for study. It should be noted that *O. olivacea* is a later homonym of *O. olivacea* Bucholtz. Therefore Harmaja (2009b) published the new name *O. olivaceobrunnea* for the illegitimate *O. olivacea*.

Otidea pusilla Rahm might be conspecific with *O. brunneoparva*, but the name is not validly published since no type was indicated (Art. 40.1 ICN) and more than one gathering was cited (Art. 40.2 ICN) (McNeill et al. 2012), ‘collected over three weeks in the same site’. The description of *O. pusilla* agrees with *O. brunneoparva* in the dark brown, cup-shaped apothecia and the relatively broad spores. The spore size given in the protologue was ‘15/6–9 *µ*’ (Rahm 1958), which we find difficult to interpret due to the unusually broad width range. Unfortunately, no material could be traced in ZH (pers. comm. R. Berndt).

A collection named by Harmaja as *O. brunneoparva* (H6017193) was found to be morphologically identical to our material. Also ITS and LSU sequences confirm that Harmaja´s and our material are conspecific. Therefore the name *O. brunneoparva* is here adopted and validated as a new species.

Otidea brunneoparva appears to be rather widespread in the Scandinavian *Picea* forests. While at least two of our collections, as indicated by Harmaja (2009a) grew on anthills, the rest were found in places with abundant *Picea* litter, often with presence of *Betula*. Two localities, including the type locality, were calcareous suggesting O. *brunneoparva* is calciphilous.

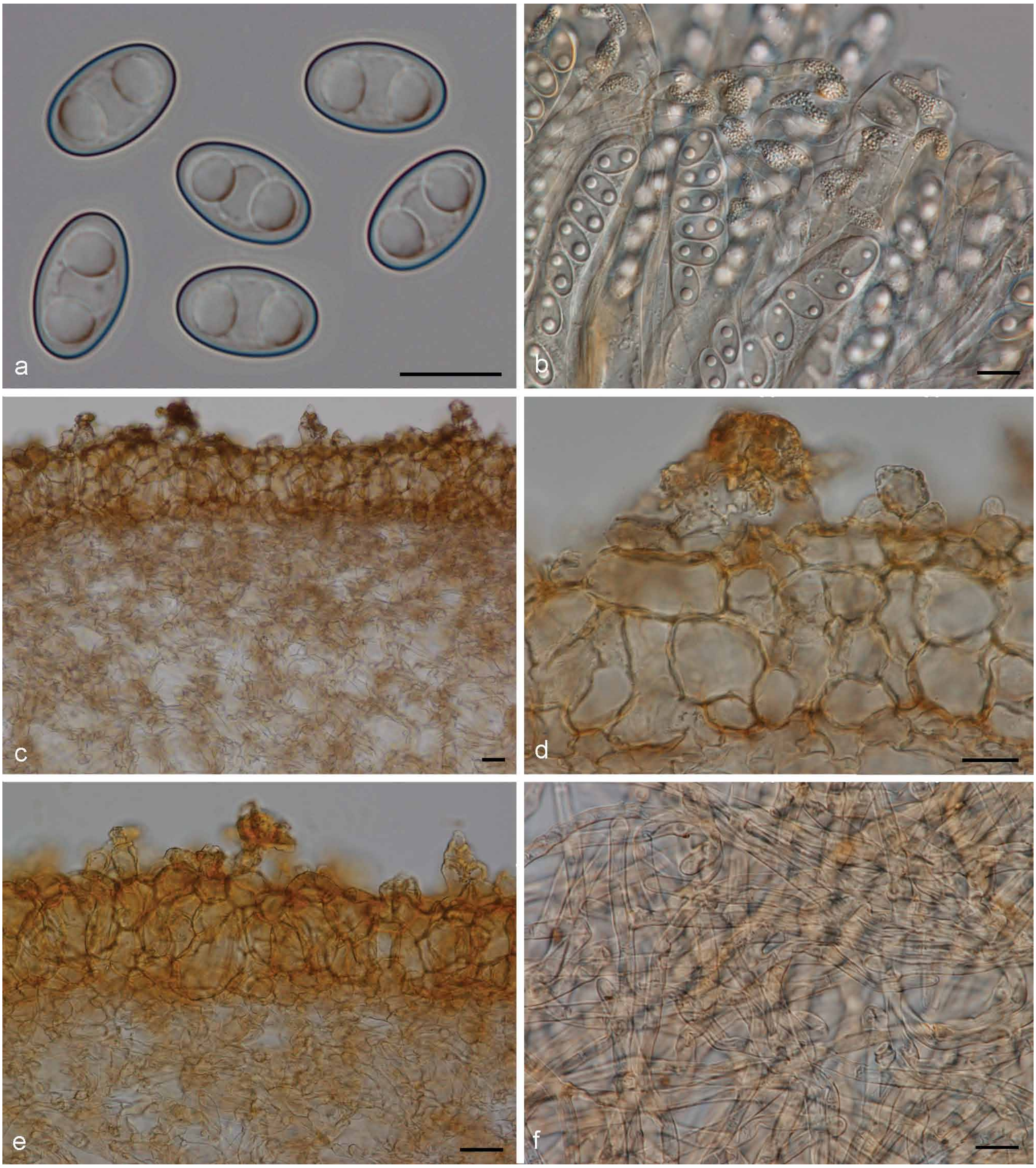

Fig. 14 *Otidea brunneoparva* (KH.08.107, holotype). a. Spores in water†; b. paraphyses*; c. medullary and ectal excipulum in water†; d. wart from the ectal excipulum in water†; e. ectal excipulum in Melzer's reagent†; f. basal mycelium in water†. — Scale bars = 10 µm; * = fresh material; † = dried material.

11. ***Otidea cantharella*** (Fr.) Quél., Enchir. Fung.: 275. 1886 — Fig. 15

Basionym. *Peziza cantharella* Fr., Syst. Mycol. 2: 48. 1822 : Fr., loc. cit.

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

Neotype designated here: SWEDEN, Jämtland, Östersund, Ändsjön Nature Reserve, in rich *Picea* forest, with *Hepatica nobilis* and *Oxalis acetosella*, 31 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.125 (S); MycoBank MBT178085.

= *Peziza caligata* Nyl., Ex Not. Sällsk. Fauna Fl. Fenn. Förh. 10: 8. 1868 '1869'.

≡ *Otidea caligata* (Nyl.) Sacc., Syll. Fung. 8: 95. 1889.

≡ *Acetabula caligata* (Nyl.) Boud., Hist. Classific. Discomyc. Europe: 41. 1907.

Holotype. FINLAND, Uusimaa, Helsinki, 1850, *W. Nylander* (H009215) !

Misapplied names

– *Otidea abietina* sensu Breitenbach & Kränzlin, Fung. Switzerland 1: 82. 1984.

– *Peziza propinquata* sensu Nannfeldt, Ann. Bot. Fenn. 3: 313. 1966.

Apothecia gregarious or caespitose, 23–68 mm high, 13–43 mm wide, initially broadly ear-shaped, in the end broadly ear-shaped to almost cup-shaped, split, stipitate. *Hymenium* initially light brown (5B5, 5B6, 5C6), then ochraceous yellow (4A5, 4A6, 5A5), ochre-orange (4A7, 5B7), sometimes with pinkish areas or red dots (6B8), when wounded pinkish and margin brownish red (6B8), when dried orange brown (6D7, 6D8) to reddish brown (6C6, 6D6). *Receptacle surface* concolorous, ochre brown (4B7, 5C7, 5B6), slightly hygrophanous, in drying yellowish ochre (4A6, 4A7), sometimes with pale brown stains, when dried orange brown (6D7, 6D8), furfuraceous to finely warty, sometimes wrinkled at the base. Warts hemispherical, gregarious, concolorous, sometimes darker than the background, brown. *Stipe* 4–25 × 3–9 mm. *Basal tomentum and mycelium* abundant, white to very pale brown (5A3), very pale brown when dried. *Spores* ellipsoid and often narrowing toward poles, sometimes very slightly inequilateral, with two large and several smaller guttules, smooth, hyaline, (17–)18–21 × (9–)10–11.5(–12) µm (L_m = 17.7–20 µm, W_m = 10.4–11.4 µm, Q_m = 1.7–1.8; n = 13). *Paraphyses* hooked, of the same width or slightly enlarged at apices, 2.5–3.5(–5.5) µm wide, without or with a low notch, seldom forked at apices, when fresh containing small, refractive, pale yellow guttules; when dried small, refractive granules. *Asci* 191–217 × 11–12 µm. *Apothecial section* 900–1200 µm thick. *Subhymenium* c. 70–100 µm thick, visible as a darker yellow zone, of cylindrical to swollen cells, densely arranged. *Medullary excipulum* of *textura intricata*, (500–)700–900 µm thick, hyphae cylindrical to slightly swollen, thick-walled, 3–12 µm wide, very pale yellow, sometimes with yellow-brown resinous exudates at septa. *Ectal excipulum* of *textura angularis* 90–120 µm, cells thin-walled, pale yellow, 23–55 × 12–25(–30) µm. Surface with conical to broadly conical warts, 55–80 µm high, formed by fasciculate, parallel, short hyphoid hairs, of 3–4 ovoid cells, constricted at septa, 5–8 µm wide. Non-warted parts with single hyphoid hairs, of 2–4 subglobose to elongated cells, slightly constricted at septa, 7–10 µm wide, sometimes with a gelatinous sheath. Resinous exudates abundant, yellow to yellow-brown, dissolving into amber drops in MLZ. *Basal my-*

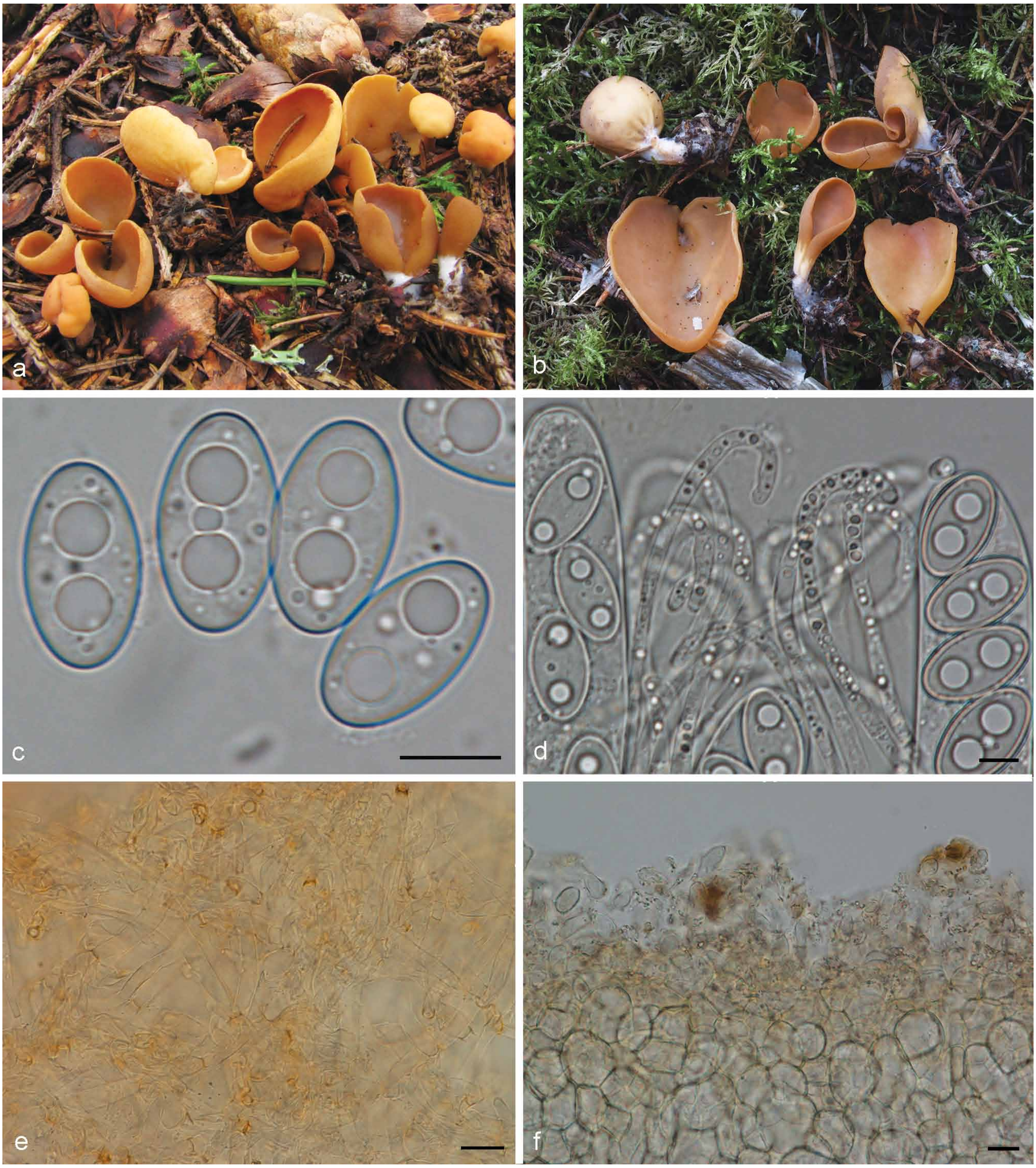

Fig. 15 *Otidea cantharella**. a, b. Apothecia; c. spores; d. paraphyses; e. medullary excipulum showing resinous exudates at septa; f. ectal excipulum (a: KH.09.125, neotype; b: KH.11.69; c, d: KH.10.152; e: KH.09.144; f: KH.09.155). — Scale bars = 10 µm; * = all fresh material.

celium of 3.5–4.5(–6) µm wide, hyaline to very pale yellowish brown hyphae, unchanged in KOH, smooth or with very small, regularly arranged, spheroid, resinous exudates, dissolving in MLZ and partially in KOH.

Specimens examined. Finland, Etelä-Häme, Hattula, Parola, Alppilankallio, *Vaccinium myrtillus*-type forest, under *Picea abies*, 25 Sept. 1967, *P. Uotila* 618 (H); Etelä-Häme, Janakkala, Tervakoski, 6 Sept. 1970, *P. Uotila* 6195 (H); Etelä-Häme, Mustiala, 5 Sept. 1895, *J. Lindroth* (H6010923); ibid., in pineto, 24 Aug. 1866, *P.A. Karsten* (H6010922); Etelä-Häme, Mustiala, Tammela, 2 Sept. 1882, *P.A. Karsten* (H6010829); Perä-Pohjanmaa, Rovaniemi, Kalkkinulkki, near old limestone quarry, under *Picea*, 23 Aug. 2011, *T. Kekki*, TK211 (TUR); Perä-Pohjanmaa, Rovaniemi, Ounasvaara, *Picea* forest, 29 Aug. 2011, *T. Kekki*, TK279 (TUR); Perä-Pohjanmaa, Rovaniemi, Välijoki, calciferous *Picea* forest, 25 Aug. 2011, *T. Kekki*, TK236 (TUR); Perä-Pohjanmaa, Tervola, Peura, old calciferous *Picea* forest, 5 Sept. 2011, *T. Kekki*, TK177 (TUR); Perä-Pohjanmaa, Ylitornio, Kuusikkorommas, calciferous *Picea* and *Pinus* forest, 2 Sept. 2011, *T. Kekki*, TK301 (TUR); Varsinais-Suomi, Vihti, Nummela, Metsäkulma, on soil, 16 Sept. 1979, *H. Kotiranta* (H6010925). – France, Isère, Villard-de-Lans, Bois Barbu, under *Picea abies*, 20 Sept. 2008, *J. Cavet*, NV 2008.09.16 (dupl. S). – Hungary, Hohe Tatra bei Unter-Schmecks, Oct. 1884, *Linhart* (UPS F-629314, Rehm Ascomyceten 251b, as *O. leporina* f. *minor*). – Italy, Trentino-Alto Adige, Cavelonte, in silvis coniferis, semper socia Cudoniae confusae, Aug. 1898, *G. Bresadola* (UPS F-629361). – Norway, Nord-Trøndelag, Steinkjer, Noem, under *Picea*, 2 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.129 (S); Nord-Trøndelag, Steinkjer, Strattåsen, in rich *Picea* forest, 5 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.144 (S). – Sweden, Blekinge, Rödeby, Spjutsbygd, c. 2 km NW from the train station, on needle litter under a *Picea* in coniferous forest, 10 Sept. 1946, *S. Lundell & S. Wikland* (UPS F-146484); Gästrikland, close to Bergby, mossy *Picea* forest on acidic ground, 31 Aug. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.152 (S); Hälsingland, Kårböle, St Olofs, 26 Aug. 2001, *H.-G. Toresson* s.n. (S); Hälsingland, south to crossing between roads E45 and 310, under *Picea abies*, among leaf litter, 21 Aug. 2011, *J.C. Zamora & I. Olariaga*, KH.11.109 (S); Härjedalen, Linsell, Djursvallen, montane coniferous forest with birch, on very rotten log, 13 Aug. 2000, *B. Gahne* (UPS F-125589); Härjedalen, Torkilstöten, under *Picea abies* among leaf litter, on acidic ground, 20 Aug. 2011, *J.C. Zamora & I. Olariaga*, KH.11.106 (S); Jämtland, Hammarstrand, *Picea* mossy forest, 26 Aug. 2009, *H. Lindström*, KH.09.83 (S); ibid., KH.09.84 (S); Jämtland, SW of Mörsil, Sandtjärndalen Nature Reserve, under *Picea abies* on rich ground, 7 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.155 (S); Jämtland, Sällsjö surroundings, in young stand of *Picea abies*, on rich ground with *Betula* and *Salix*, 29 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.104 (S); Jämtland, Östersund, Andersön Nature Reserve, *Picea* forest on rich ground, 28 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.95 (S); ibid., under *Picea* and *Pinus*, KH.09.96 (S); ibid., KH.09.101 (S); Jämtland, Östersund, Fillstabäcken Nature Reserve, on old anthill under *Picea*, *K. Hansen & I. Olariaga*, 30 Aug. 2009, KH.09.111 (S); ibid., KH.09.117 (S); ibid., *K. Hansen & X.H. Wang*, 5 Sept. 2012, KH.12.99 (S); Jämtland, Östersund, Ändsjön Nature Reserve, in rich *Picea* forest, with *Hepatica nobilis* and *Oxalis acetosella*, 26 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.78 (S); ibid., KH.09.80 (S); ibid., KH.09.98 (S); Jämtland, Åre, Kall, along Stor-Grundsviken, Kallsjön, on old anthill in lime rich *Picea* forest, 15 Aug. 2008, *J. Santos & K. Hansen*, JS.08.18 (S); Lappland, Jokkmokk, SE of Vuollerim, Andersviksravinerna (Natura 2000 area), mixed forest, 31 Aug. 2011, *A. Stridvall*, KH.11.111 (S); ibid., KH.11.112 (S); Lappland, Jokkmokk, by Kassavare mountain, Köpenhamn, under *Picea abies*, 1 Sept. 2011, *K. Hansen & I. Olariaga*, KH.11.110 (S); Lappland, Jokkmokk, 'Nornaskogen' by Ållojaur, mossy *Picea* forest on rich ground, 29 Aug. 2011, *K. Hansen & I. Olariaga*, KH.11.16 (S); Lappland, Kuouka, 15 km SE Messaure, herb-rich *Picea* forest on rich ground, among mosses, 3 Sept. 2011, *K. Hansen & I. Olariaga*, KH.11.68 (S); ibid., KH.11.69 (S); Lappland, 5 km SE Vuollerim, part of Andersviksravinerna, Rävabacken Nature Reserve, herb-rich *Picea* forest, 21 Aug. 2000, *M. Karström*, MK200061 (S); ibid., under *Picea* on mossy ground, together with *Cudonia confusa*, 2 Sept. 2011, *K. Wiking*, KH.11.59 (S); Småland, Ryssby, Gärdsholmen, Björnö, coniferous forest, 6 Sept. 1930, *H.G. Bruun* (UPS F-146485); ibid., on deep moss in coniferous forest (UPS F-146486); Uppland, Uppsala, Sävja, Norra Lunsen Nature Reserve, *Picea* forest, on soil, thick layer of litter and mosses, 28 Aug. 2008, *J. Santos*, JS.08.47 (S). – Switzerland, Wallis Canton, Liddes, Palazuit, in side of brook under *Picea abies*, 17 Aug. 2008, *M. Carbone* (MCVE 24217).

Notes — *Otidea cantharella* can be recognised by broadly ear-shaped apothecia, with yellow to orange tones, often with a well-developed stipe, and large spores. No other species of *Otidea* have the spore size of *O. cantharella*, in combination with those macroscopic characters.

Otidea cantharella is associated with *Picea abies*, and often produces apothecia on anthills or thick needle layers. Furthermore, we have often found apothecia of *O. cantharella* and *Cudonia confusa* together (Fig. 15a), and once with *Spathularia rufa*, both species belonging to the *Rhytismatales*. An apparent closer association in the same fairy ring has also been observed once. Interestingly, Bresadola noted the association with *C. confusa* in one of his collections (UPS F-629361) studied by us. The presence of *C. confusa* in the same collecting spot may give a first plausible field identification of *O. cantharella*. Moreover, it suggests a possible biotrophic association between *O. cantharella* and *C. confusa*.

Nomenclatural notes — This species has been referred to as *O. caligata* (Nyl.) Sacc. (Nannfeldt 1966, Dissing 2000). Nevertheless, Harmaja (2009a) came to the conclusion that the name *O. cantharella* must refer to the large-spored species treated here, with which some authors have later disagreed (Carbone 2010b, Van Vooren 2011b). Harmaja stressed the following characters from the protologue supporting the usage of the name as presented here: ear-shaped, stipitate apothecia, the yellow colour of *Cantharellus cibarius* and the occurrence in *Picea* forests in southern Sweden. We have studied material from Småland (UPS F-146485, UPS F-146486), from where Fries described *O. cantharella*. It is therefore very likely that Fries had in mind the species described here when he coined the name *O. cantharella*, although he had only seen dried material, as indicated by the abbreviation '*v. s.*' (*vidi siccam*, seen dried). Since no original material is known to exist, we propose a neotype that will attach the name *O. cantharella* to the *Otidea* species described here. This stabilises the interpretation proposed by Harmaja (2009a), also used by Mornand & Courtecuisse (2005), and long before adopted by Bresadola (1900: 102), and should serve to settle the interpretation of *O. cantharella*. Our ITS-LSU sequences of four *O. cantharella* collections from Sweden and France are identical.

12. *Otidea propinquata* (P. Karst.) Harmaja, Karstenia 15: 32. 1976 — Fig. 16

Basionym. *Peziza propinquata* P. Karst., Not. Sallsk. Fauna Fl. Fenn. Forh. 10: 110. 1869.

Lectotype. Finland, Tavastland, Messuby, 7 Oct. 1860, *P.A. Karsten* (H6010807) !, selected by Nannfeldt (1966).

= *Otidea abietina* f. *nigra* Rick, Oesterr. Bot. Z. 48: 62. 1898.

≡ *Otidea abietina* var. *nigra* (Rick) Sacc., Syll. Fung. 14: 746. 1899.

Lectotype. Austria, Vorarlberg, an der Gamp, im Nadelwald, 1700 m, Sept. 1897, *Rick* (S-F9962) !, indicated by Nannfeldt (1966).

= *Otidea indivisa* Velen., Monograph. Discom. Bohemiae 1: 355. 1934.

Lectotype. Czech Republic, Karlštejn N, Oct. 1922, *J. Fechtner* (PRM 149147) !, selected by Nannfeldt (1966).

Misapplied names

– *Pseudotis abietina* sensu Boudier, Icon. Mycol. livr. 7: nº. 131, pl. 333. 1906 (preliminary text with 'circulaires').

– *Otidea cochleata* sensu Breitenbach & Kränzlin, Fung. Switzerland 1: 84. 1984.

Apothecia gregarious or caespitose, 7–20 mm high, 15–35 mm wide, obconical to broadly cup-shaped, entire, very rarely split, regular or sometimes undulate in the margin, stipitate. *Hymenium* ochre brown (5C7, 6D5, 6D6) to dark reddish brown (6F6, 6F7, 7F7, 7F8), when dried ochre brown (6B7, 6C7). *Receptacle surface* concolorous, orange brown (6F6, 6F7), slightly hygrophanous, in drying yellowish brown (5C6, 5C7), when dried orange brown (6D6, 6D7, 6E7), furfuraceous to warty, sometimes wrinkled at the base. Warts hemispherical, gregarious, concolorous, sometimes darker than the background, brown. *Stipe* 7–16 × 2–7 mm. *Basal tomentum and mycelium* abundant, white to very pale brown (5A3), very pale brown when dried. *Spores* ellipsoid and often narrowing toward

Fig. 16 *Otidea propinquata*. a. Apothecia; b. spores in water†; c. paraphyses in KOH†; d. wart of the ectal excipulum in water†; e. ectal excipulum in KOH†; f. basal mycelium in water† (a: KH.11.21; b–f: KH.09.99). — Scale bars = 10 µm; † = dried material.

the poles, sometimes very slightly inequilateral, with two large and several smaller guttules, smooth, hyaline, (18–)19–21 × 10–12.5 µm (L_m = 19.3–20 µm, W_m = 10.9–11.6 µm, Q_m = 1.6–1.7; n = 4). *Paraphyses* hooked, of the same width or often enlarged at apices, 3–5 µm wide, often with 1–3 notches or forked at apices, when fresh containing small, refractive, light yellow guttules; when dried hyaline. *Asci* 231–275 × 12–16 µm. *Apothecial section* 1100–1500 µm thick. *Subhymenium* c. 100–120 µm thick, of dense *textura intricata*, visible as a darker brown zone. *Medullary excipulum* of *textura intricata*, 600–800 µm thick, hyphae 4–9 µm wide, sometimes slightly swollen, thin- to thick-walled, very pale brown, sometimes with brown resinous exudates at septa. *Ectal excipulum* of *textura angularis* 100–130 µm, cells rather thick-walled, pale brown, 17–50 × 10–40 µm. Surface with conical to broadly conical warts, 50–75 µm high, formed by short, fasciculate hyphoid hairs, of 2–3 subglobose to elongated cells, constricted at septa or not, 8–11 µm wide, sometimes with a pale brown thick gelatinous sheath. Resinous exudates abundant, yellow-brown to brown, turning brownish red in KOH, dissolving in MLZ. *Basal mycelium* of 3–6 µm wide, hyaline to pale brown hyphae, unchanged in KOH, smooth or normally with regularly arranged, spheroid to rod-shaped, resinous exudates, dissolving in MLZ and partially in KOH.

Specimens examined. Czech Republic, Praha, Karlštejn, 9 Oct. 1922, *F. Fechtner* (UPS F-629369, syntype of *O. indivisa*); Sept. 1924 (UPS F-629367, syntype of *O. indivisa*). – Denmark, NE Sjælland, Asserbo Plantage, under *Pinus* and *Picea* among needles, 7 Oct. 1975, *H. Knudsen* (C-F-87203).

– France, Isère, Lans-en-Vercors, on the ground, on *Picea* leaf litter, 17 Sept. 2008, *J. Cavet*, NV 2008.09.15 (dupl. S). – Italy, Trentino-Alto Adige, Sopramonte, ad acus abiegnos in sylvis coniferis, Aug. 1898, *G. Bresadola* (UPS F-629357). – Sweden, Jämtland, Sällsjö surroundings, in young stand of *Picea abies*, on rich ground, 28 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.99 (S); Jämtland, Östersund, Andersön Nature Reserve, under *Pinus* and *Picea*, on rich ground, among mosses, 28 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.94 (S); ibid., KH.09.103 (S); Jämtland, Östersund, Ändsjön Nature Reserve, in rich *Picea* forest, 26 Aug. 2009, *K. Hansen & I. Olariaga*, KH.09.81 (S); ibid., 31 Aug. 2009, KH.09.123 (S); Lappland, Jokkmokk, 'Nornaskogen' by Ållojaur, mossy *Picea* forest on rich ground, 28 Aug. 2011, *K. Hansen & I. Olariaga*, KH.11.21 (S); Lappland, Jokkmokk, Ultevis Fjällurskog Nature Reserve, Sitoätno, *Picea* mossy forest on rich ground, among leaf litter, 31 Aug. 2011, *K. Hansen & I. Olariaga*, KH.11.30 (S); ibid., KH.11.35 (S); Lappland, S of Kvikkjobb-Kabla FUR Nature Reserve, by Kassavare mountain, Köpenhamn, young *Picea* stand by a road, 1 Sept. 2011, *K. Hansen & I. Olariaga*, KH.11.53 (S); Lappland, Messaure, herb-rich *Picea* forest, 29 Aug. 2008, *M. Karström*, MK0834 (S); Lappland, 17 km WSW of Vuollerim, Slubbojaureskogen, herb-rich *Picea* forest, 8 Aug. 2002, *M. Karström*, MK0222 (S); Närke, Knista, Lekhyttan, under *Picea*, in thick litter layer, in lime rich forest, 12 Sept. 2008, *J. Santos*, JS.08.67 (S); Uppland, Uppsala, Sätra Nature Reserve, on litter on lime rich soil, under *Picea*, 23 Sept. 2008, *J. Santos & K. Hansen*, JS.08.98 (S). – USA, Washington, Lake Crescent, under fir, 28 Oct. 1935, *A.H. Smith* (UPS F-629351).

Notes — *Otidea propinquata* is easily recognised by the stipitate, entire, brown apothecia, large spores, and notched or forked paraphyses. *Otidea daliensis* shares brown, entire apothecia with *O. propinquata*, but differs in having sessile apothecia, with purplish brown tones, and basal mycelium that lacks abundant resinous exudates.

There has been uncertainty surrounding the correct name of this taxon. A number of early authors used the epithet *abietina* to refer to *O. propinquata* (Boudier 1906, Bresadola 1933). In agreement with Harmaja (2009a) and Carbone (2010c), we consider *Peziza abietina* a *nomen confusum*. Nannfeldt (1966) referred to *O. propinquata* as *O. indivisa* and argued that the type of *O. propinquata* was conspecific with *O. cantharella* (as *caligata*). Harmaja (1976) examined the lectotype of *O. propinquata* and found it to be clearly distinct from *O. cantharella* and *O. indivisa*, a later synonym. This is confirmed by our study of the type of *O. propinquata*. *Otidea propinquata* occurs in *Picea* forests on calcareous ground. It is widespread in Northern Fennoscandia and present in central Europe.

Otidea formicarum clade

Apothecia ear- to cup-shaped, split, ochre to reddish brown. Spores small, 9.5–12 µm long. Basal mycelium with abundant yellow resinous exudates. Associated with conifers.

Species — *Otidea formicarum*, *O. nannfeldtii*, *O. subformicarum*, *O.* aff. *subformicarum*, *Otidea* sp. 'b'.

13. *Otidea formicarum* Harmaja, Karstenia 15: 31. 1976 — Fig. 5f, 17

Holotype. Finland, Etelä-Karjala, Miehikkälä, Savanjärvi, on anthill in spruce forest, 26 Sept. 1970, *L. Fagerström* (H6003549) !

Apothecia gregarious to caespitose, 8–22 mm high, 5–20 mm wide, broadly ear-shaped, upper margin rounded, then expanding and sometimes in the end becoming cup-shaped and flattened, split, stipitate or sessile. *Hymenium* yellowish brown (5C7, 5C8) to reddish brown (6C7, 6C8, 6D8), when dried ochre (4A5, 4A6) to brownish ochre (5B7). *Receptacle surface* yellowish brown (5C6) to reddish brown (6C6), hygrophanous, in drying ochre (5B7), when dried ochre (4A5, 4A6), finely warty, smooth at the base. Warts broadly conical to rounded, gregarious, concolorous, sometimes slightly darker than the background, brown. *Stipe* 3–6 × 2–4 mm. *Basal tomentum and mycelium* abundant, light yellow-ochre (5A2). *Spores* ellipsoid, seldom very slightly inequilateral, with two large guttules, smooth, hyaline, 9.5–11(–11.5) × (5.5–)6–7 µm (L_m = 10–10.7 µm, W_m = 6–6.9 µm, Q_m = 1.6–1.7; n = 7). *Paraphyses* curved to hooked, of the same width or slightly enlarged at apices, 3–4 µm wide, with up to two slightly swollen areas, occasionally notched, sometimes when fresh containing small, refractive, light yellow or green guttules; when dried small, refractive, hyaline to light yellow granules. *Asci* 160–232 × 10.5–13 µm. *Apothecial section* 700–800 µm thick. *Subhymenium* c. 80–100 µm thick, of dense *textura intricata*, visible as a yellowish brown zone, cells cylindrical to swollen, densely arranged. *Medullary excipulum* 400–500 µm thick, differentiated into two parts: a) *textura angularis* underneath the subhymenium, 120–200 µm thick, cells 6–15 µm broad; b) *textura intricata*, hyphae sometimes slightly swollen, thin-walled to thick-walled, 3–11 µm wide, hyaline to very pale yellow, sometimes with pale yellow resinous exudates at septa. *Ectal excipulum* of *textura angularis*, 70–120 µm, cells thin-walled, light yellow, 17–40 × 11–25 µm. Surface with broadly conical warts, 45–60 µm high, formed by short, fasciculate, hyphoid hairs, of 2–3 elongated cells, 7–12 µm wide, not or slightly constricted at septa, sometimes with a gelatinous sheath. Resinous exudates abundant, brownish yellow, dissolving into amber drops in MLZ. *Basal mycelium* of 3–5 µm wide, hyaline to very light yellow hyphae, unchanged in KOH, with regularly arranged, very small, spheroid resinous exudates, dissolving in MLZ, partially and more slowly in KOH.

Specimens examined. Finland, Etelä-Häme, Lammi, Evo, Vahtervehmas, Kotinen virgin forest, 6 Sept. 1988, *H. Harmaja* (H6003551); Etelä-Häme, Loppi, Topeno, Piimästennummi, on a huge anthill, under *Picea*, 16 Sept. 2011, *S. Huhtinen* 11/65 (TUR); Perä-Pohjanmaa, Rovaniemi, Välijoki, calciferous *Picea* forest, on anthill, 25 Aug. 2011, *T. Kekki*, TK223 (TUR); Uusimaa, Elimäki, Villikkala, Lääksynmäki, mesic heath spruce forest, on anthill, 22 Oct. 2005, *U. Nummela-Salo & P. Salo* (H6003550); Varsinais-Suomi, Koski Tl., Hongisto, on old anthill under *Picea abies*, with *Betula* sp., *Salix caprea* and *Pinus sylvestris*, 8 Aug. 1998, *M.-L. & P. Heinonen* (TUR 124728); Varsinais-Suomi, Lieto, Suopohja, SE of Päivärinne, along the road by the house Esko-Ukura, on old anthill under *Picea abies*, 2 Oct. 2009, *K. Ruottinen* (TUR-A 183242). – France, Haute Savoie, Thorens-Glières, plateau des Glières, under *Picea*, on the ground, 22 Sept. 2006, *L. Francini*, NV 2006.09.11 (S). – Norway, Nordland, Grane, Holmvassdalen Nature Reserve, on old anthill under *Picea*, 29 Oct. 2009, *J. Lorås* (S-F244372). – Sweden, Dalarna, Stora Tuna, between Falubäcken and Övre Morbygge fäbod, abundant in the lower part of an active anthill, 22 Sept. 1963, *R. Morander* (UPS F-146725); Närke, Askersund, Orkarebäckens Nature Reserve, calcareous forest, on an active anthill under *Picea*, 11 Sept. 2008, *J. Santos*, JS.08.63 (S); ibid., under *Picea* in litter, JS.08.62 (S); Uppland, Bondkyrka, Gottsundabergen, 1 Oct. 1927, *J.A. Nannfeldt* (UPS F-146706); Uppland, Bondkyrka, Nåsten, S of Läbyvad station, among coniferous needles, 16 Sept. 1932, *J.A. Nannfeldt* (UPS F-146709); Uppland, Älvkarleby, Billuddens Nature Reserve, under *Pinus* and *Picea* on sandy ground, at the base of a *Pinus*, 15 Sept. 2011, *J.C. Zamora & I. Olariaga*, KH.11.104 (S); Ångermanland, Ullanger, Håll, in the eastern slope of Mt Moberget, c. 0.5 km SW of p. 35,29, on the ground, 14 Sept. 1974, *R. Moberg* (UPS F-146735).

Notes — *Otidea formicarum* is characterised by relatively small, reddish brown, broadly ear-shaped apothecia, small spores, and by its habitat, often occurring on anthills. For a comparison with the sister species *O. subformicarum* see under that species below. *Otidea nannfeldtii* resembles *O. formicarum*, but differs in often having more narrowly ear-shaped and paler coloured apothecia, sometimes with pink tones in the hymenium. Dried apothecia of *O. nannfeldtii* have, on the contrary, darker colours than *O. formicarum*. *Otidea pseudoleporina* and *O. formicarum* share apothecial shape, but *O. pseudoleporina* can be distinguished by the ochre-orange colour, and comparatively narrower spores (Q_m = 1.7–1.9).

The original description of *O. formicarum* was based on several collections made on anthills in Finland (Harmaja 1976), and more recent material has been cited from anthills (Harmaja 2009a, b), mainly associated with *Picea*. Most of the material examined by us was also from anthills, but at least one of our Swedish finds (KH.11.104) was from *Pinus* needle litter, which shows the habitat of *O. formicarum* partly overlaps with the habitat of *O. subformicarum*.

14. ***Otidea nannfeldtii*** Harmaja, Karstenia 15: 31. 1976 — Fig. 5a, d, 18

Holotype. Finland, Ahvenanmaa, Lemland, Nåtö, spruce forest near Övergård, 17 Sept. 1972, *C.-A. Haeggström* (H6002902) !

= *Otidea angusta* Harmaja, Karstenia 48: 35. 2009.

Holotype. Finland, Varsinais-Suomi, Lohja, Jalassaari, Ahtiala, E of Heimo house, mixed somewhat moist rich woods with *Picea*, *Betula*, *Corylus* etc. on somewhat calcareous soils, 23 Aug. 1965, *H. Harmaja* (H6010804) !

Misapplied names

– *Otidea papillata* sensu Van Vooren et al., Bull. Mycol. Bot. Dauphiné-Savoie 188: 52. 2008.

Apothecia gregarious to caespitose, 8–35 mm high, 5–15 mm wide, initially long, narrowly ear-shaped, sometimes expanding and becoming broadly ear-shaped, split, stipitate or sessile. *Hymenium* ochre (4A5), orangish ochre (5B4, 5C4) or pale brown (6D6, 6D7), sometimes with pink tones or entirely pinkish (6A4), when dried orange-ochre (5A5) to reddish brown (6C6). *Receptacle surface* brown orange (5B4, 5C4) to pale brown (6D6–7), slightly hygrophanous, in drying ochre (4A5), when dried reddish brown (7D7, 7E7), finely warty, smooth at the base. Warts conical, gregarious, concolorous, sometimes distinctly darker than the background, brown. *Stipe* 4–8 ×

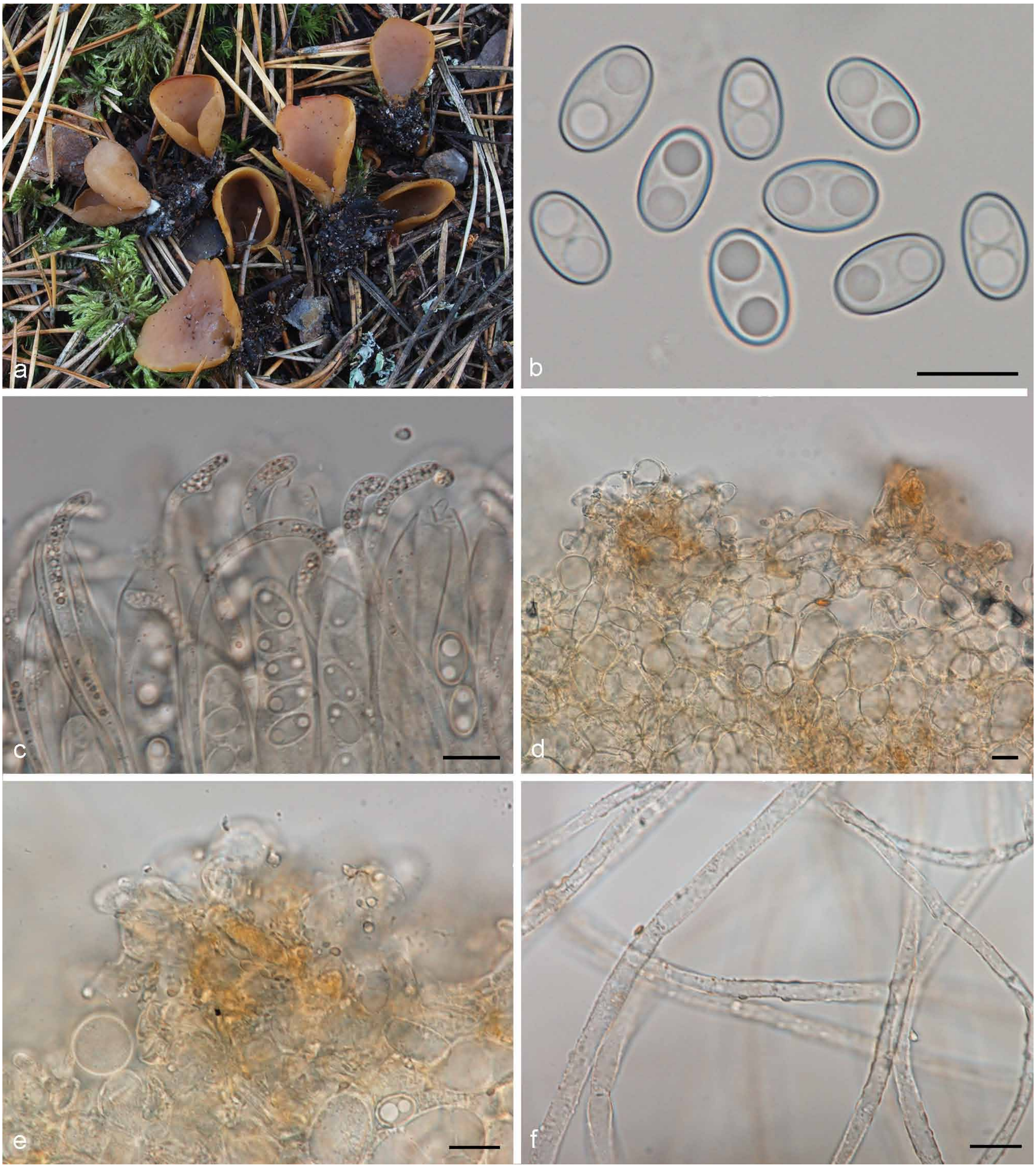

Fig. 17 *Otidea formicarum* (KH.11.104)*. a. Apothecia; b. spores; c. paraphyses; d. ectal excipulum; e. resinous exudates of the ectal excipulum; f. basal mycelium. — Scale bars = 10 µm; * = all fresh material.

2–3 mm. *Basal tomentum and mycelium* abundant, white to light yellow (5A2) or ochre (5A3). *Spores* ellipsoid, sometimes slightly inequilateral, with two large guttules, smooth, hyaline, (9–)9.5–10.5(–11.5) × 5.5–6.5(–7) µm (L_m = 9.8–10.9 µm, W_m = 5.5–6.6 µm, Q_m = 1.6–1.9; n = 10). *Paraphyses* curved to hooked, of the same width or slightly broader at apices, 2.5–5 µm wide, without notches, rarely with up to two slightly swollen areas or forked at apices, when fresh containing small, refractive, light yellow guttules; when dried hyaline to light yellow. *Asci* 137–190 × 8–10 µm. *Apothecial section* 650–900 µm thick. *Subhymenium* c. 80–100 µm thick, visible as a yellowish brown zone, of cylindrical to swollen cells, densely arranged. *Medullary excipulum* of *textura intricata*, 400–600 µm thick, differentiated into two parts: a) *textura angularis* underneath the subhymenium, 100–150 µm thick, cells 13–32 × 12–21 µm; b) *textura intricata*, 400–450 µm thick, hyphae 4–9 µm wide, thin-walled to slightly thick-walled, hyaline to very pale yellow, sometimes with pale yellow resinous exudates at septa. *Ectal excipulum* of *textura angularis*, sometimes of a *textura prismatica*, 80–120 µm, cells thin-walled, hyaline to light brown, 16–40 × 11–22 µm. Outer part of conical to broadly conical warts, 45–85 µm high, formed by short, fasciculate, hyphoid hairs, of 2–3(–4) subglobose to elongated cells, constricted at septa, 5–9 µm wide, sometimes with a gelatinous sheath. Resinous exudates abundant, yellow brown, dissolving into amber drops in MLZ, reddish brown in KOH. *Basal mycelium* of 3–5.5 µm wide, septate, hyaline to very light yellow hyphae, unchanged in KOH, with very small, regularly arranged, spheroid, yellow resinous exudates, dissolving in MLZ, partially and more slowly in KOH.

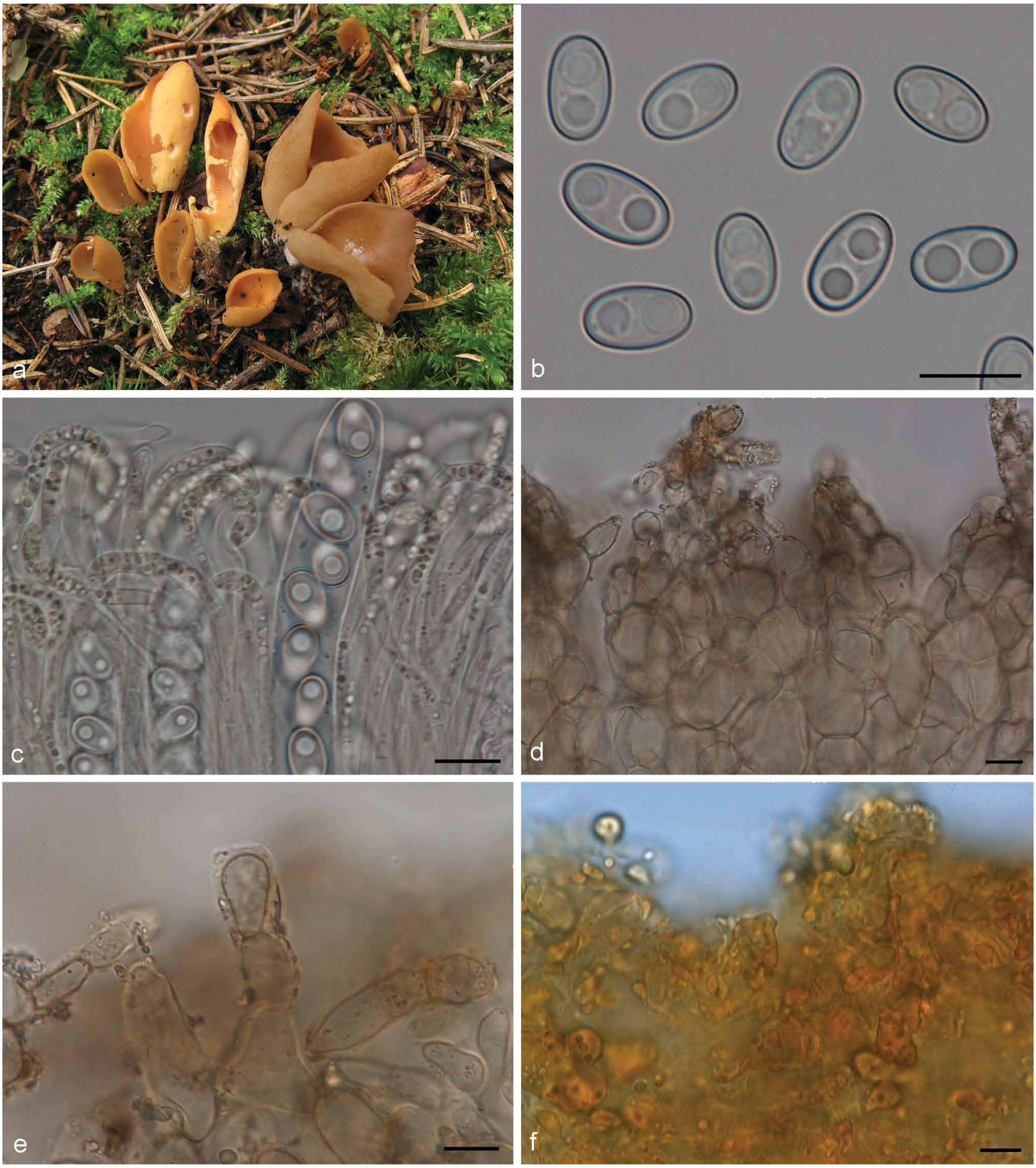

Fig. 18 *Otidea nannfeldtii*. a. Apothecia; b. spores*; c. paraphyses*; d. ectal excipulum*; e. hyphoid hairs with gelatinous sheath*; f. amber drops on the outermost ectal excipulum cells in Melzer's reagent† (a–e: KH.10.302; f: S-F249387). — Scale bars = 10 µm; * = fresh material; † = dried material.

Specimens examined. Finland, Varsinais-Suomi, Lohja, Jalassaari, Ahtiala, Alho, very close to the Ahtiala Nature Reserve, below a spruce tree in mixed forest on fairly calcareous soil, 29 Sept. 1978, *H. Harmaja* (S-F249387, ex H6017194 as *O. lohjaënsis* nom. prov.). – France, Hautes Alpes, Provence-Alpes-Côte-d'Azur, La Bâtie-Montsaléon, Les Chariots du Buech, au sol dans la litière d'aiguilles de pins (*P. sylvestris*), 26 Oct. 2008, *N. Van Vooren*, NV 2008.10.01 (dupl. S). – Italy, Abruzzo, Pietracamela (TE), Prati di Tivo, on soil in mixed forest, mainly with *Larix* but also *Picea* and *Pinus*, 2 Oct. 2009, *B. De Ruvo* (S-F257096); Calabria, Celico (CS), Contrada Colamauci, under *Pinus* and *Picea abies*, 16 Sept. 2009, *C. Lavorato*, CL 091116-17 (dupl. S); Calabria, Morano Calabro (CS), Campotenese, under *Pinus sylvestris*, 7 Dec. 2009, *C. Lavorato*, CL 091207-01 (dupl. S). – Sweden, Gotland, Ollajvs Nature Reserve, close to Ljugarn, under *Picea* and *Pinus* on calcareous ground, 31 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.302 (S); ibid., under *Picea* and *Pinus* on rich calcareous soil, 27 Sept. 2011, *H. Tuovila & S. Huhtinen*, KH.11.115 (S); Lappland, Jokkmokk, 'Nornaskogen' by Ållojaur, under *Picea* among mosses, *K. Olofsson*, 1 Sept. 2011, KH.11.45 (S); Lappland, Messaure, 3 miles NW Vuollerim, herb rich *Picea* forest, 1 Sept. 2005, *M. Karström*, MK0536 (S); Lappland, Västra Tjetnekbäcken, 9 km E of Jokkmokk, under *Picea abies*, *K. Olofsson*, 1 Sept. 2011, KH.11.112 (S); Uppland, Stockholm, Enebyberg, Rinkebyskogen, on soil under *Picea* and deciduous trees in side of footpath, 29 Sept. 2008, *J. Santos*, JS.08.103 (S). – USA, Oregon, Douglas Co., Thielsen Creek, under conifers, 13 Oct. 2010, *R. Helliwell*, rh101310 (OSC).

Otidea cf. *nannfeldtii* — Denmark, Løvenholm Skov, Langsø, 25 km W of Grenaa, 30 Sept. 1968, *H. Folkmar* (C-F-48295), (C-F-48296), (C-F-48297).

Notes — *Otidea nannfeldtii* is characterised by ochre to light brown, narrowly ear-shaped apothecia, small spores and resinous exudates on the ectal excipulum turning reddish brown in KOH. It resembles other species with ear-shaped apothecia and small spores, such as *O. formicarum*, *O. papillata*, *O. pseudoleporina* and *O. tuomikoskii*. The most similar species is *O. formicarum* (see under *O. formicarum*). *Otidea tuomikoskii* is separated from *O. nannfeldtii* by higher and more densely placed warts on the apothecial outer surface, along with the yellow reaction of the excipulum in KOH. *Otidea pseudoleporina* has a brighter ochre-orange hymenium, and the resinous exudates of the outer excipulum only partly convert into reddish grey heterogeneous drops in KOH.

Otidea nannfeldtii, as treated here, shows some phylogenetic structure (Fig. 1; but see Hansen & Olariaga 2015). Recently *O. angusta* was described as distinct from *O. nannfeldtii*, based on a few subtle characters, i.e. taller and slightly thicker fleshed apothecia, with very faintly brownish basal mycelium, paraphyses with shorter and thinner apical cells, and maybe smaller spores (Harmaja 2009a). At that time only a single collection of each species was known. Based on studies of additional collections, we did not find correlations between any morphological characters and the subgroups supported by our multiple molecular phylogenies. Therefore, we propose *O. angusta* be placed in synonymy with *O. nannfeldtii*. Supporting this, our study of the holotype of *O. angusta* revealed larger spores (9.5–11 × 5–5.8 µm) than cited in the protologue (8–9.8 × 4.5–5.2 µm), and broader paraphyses (2–3 µm) with longer terminal cells (up to 67 µm). We have also observed both tall, narrow and rounded apothecia of *O. nannfeldtii* in the same spots, and we consider the apothecial shape to vary during development. *Otidea lohjaënsis*, proposed by Harmaja (2009a) as a provisional name, is also suggested to be conspecific with *O. nannfeldtii*. A collection identified by Harmaja as *O. lohjaënsis* (S-F249387, ex-H6017194) showed excipular resinous exudates dissolving into amber drops in MLZ (Fig. 18f), contrary to the key character given for *O. lohjaënsis* (i.e. not responding to MLZ). The variation in the ITS region within *O. nannfeldtii* as recognised here is high, but displays no length variation (alignment 790 bp long). The ITS sequences of the Finnish holotypes of *O. angusta* and *O. nannfeldtii* show 26 bp differences. At the same time, however, the ITS sequence of the Swedish KH.10.302 shows 33 and 32 bp differences from the *O. nannfeldtii* and *O. angusta* holotypes, respectively. The North American rh101310 shows 14 and 20 bp differences from the two holotypes, *O. nannfeldtii* and *O. angusta*, respectively. The collections showing no LSU sequence variation (Fig. 1), show also no, or only 1–2 bp differences in the ITS region. No variation was found between the holotype of *O. angusta* and the Finnish S-F249387 (identified as the provisional *O. lohjaënsis* by Harmaja).

Otidea nannfeldtii was previously known only from South West Finland (Harmaja 1976, 2009a). Here we report it from other areas in Europe, and for the first time from North America.

15. ***Otidea subformicarum*** Olariaga, Van Vooren, M. Carbone & K. Hansen, *sp. nov.* — MycoBank MB809252; ITS barcode GenBank: KM010054; Fig. 19, 21

Etymology. Referring to its similarity to *O. formicarum*.

Holotype. Spain, Huesca, Bielsa, Ermita de Nª Señora de Pineta, 1270 m, 42.638039, 0.180532 (decimal format), under *Pinus sylvestris* and *Abies alba* on calcareous ground, 13 Oct. 2012, *J.C. Campos & J. Herranz* (S-F242696).

Apothecia gregarious to caespitose, 13–32 mm high, 10–20 mm wide, broadly ear-shaped, soon becoming deeply cup-shaped, split, margin sometimes lobate, sessile or stipitate. *Hymenium* orange brown (6C6, 6C8) to dark reddish brown (6D7, 6D8), slightly hygrophanous, when dried orange brown (7A8). *Receptacle surface* orange brown (6B7, 6C7) to reddish brown (6D8), hygrophanous, in drying orange ochre (6A6, 6A7), when dried ochre brown (5B6), brown (6C8) or reddish brown (7D8), finely furfuraceous, smooth at the base. Warts present near the margin, flat and rounded, concolorous, brown. *Stipe* 3–4 × 2–3 mm. *Basal tomentum and mycelium* pale yellow (4A3). *Spores* ellipsoid, slightly inequilateral, with two large guttules, rarely with one to several smaller granules, smooth, hyaline, 10.5–12 × 6–6.5 µm (L_m = 11.1–11.7 µm, W_m = 6.1–6.7 µm, Q_m = 1.7–1.9; n = 4). *Paraphyses* broadly hooked, sometimes curved, sometimes enlarged at the apices to 2.5–3 µm wide, without notches, sometimes with a brown matter covering the apices, when fresh containing small, pale yellow guttules; when dried heterogeneous, pale yellow. *Asci* 184–237 × 11–11.5 µm. *Apothecial section* 800–1200 µm thick. *Subhymenium* c. 100–150 µm thick, of dense *textura intricata*, with tendency to *textura angularis* towards the medullary excipulum, visible as a darker orange brown zone, cells 2.5–6(–15) µm wide, with scattered brown resinous exudates. *Medullary excipulum* 300–700 µm thick, of *textura intricata*, hyphae thin-walled to slightly thick-walled, 3–12 µm wide, very pale yellow to pale brownish yellow, sometimes with brown resinous exudates at septa. *Ectal excipulum* of *textura angularis*, (85–)100–120 µm, cells thin-walled, very pale brown, (9–)17–22(–35) × (6–)11.5–23 µm. Surface with narrowly to broadly conical warts, 45–65 µm high, formed by short, fasciculate, hyphoid hairs, of 2–3 cylindrical to ovoid cells, 7–10 µm wide, not or slightly constricted at septa. Non-warted areas with single hyphoid hairs, of 2–3 cylindrical to ovoid cells, (5–)7–12 µm wide, not or slightly constricted at septa, sometimes with a gelatinous sheath. Resinous exudates abundant, pale yellowish brown, dissolving into amber drops in MLZ, turning slightly darker and partly dissolving in KOH. *Basal mycelium* of 2–5.5 µm wide, hyaline to very light yellow hyphae, unchanged in KOH, with refractive, pale yellow drops on the surface, dissolving in MLZ.

Specimens examined. Italy, Cosenza, Calabria, Colamauci, Celico, under *Pseudotsuga menziesii*, *C. Lavorato*, 28 Sept. 2005, CL 050928-30 (dupl. S-F256978). – Spain, Canary Islands, La Palma, under *Pinus canariensis*, 26 Nov. 2008, *J. Fernández Vicente*, *P. Iglesias*, *F. Hidalgo*, *J.R. Undagoitia*, *S. Lequerica* & *R. Martínez* (S-F256979); La Rioja, Clavijo, under *Pinus sylvestris*, on the ground, *C.M. Pérez del Amo & R. Gil*, 3 Jan. 2009, private herb. CMP 1179, RM 1095 (dupl. S-F256980); Madrid, Bustarviejo-Canencia, Puerto de Canencia, 3 Oct. 1979, *E. Álvarez* (AH44526).

Fig. 19 *Otidea subformicarum* apothecia. a. S-F242696, holotype; b. S-F256980; c. S-F256979; d. CL 050928-30. — Photos: b. C. Pérez del Amo; c. J. Fernández Vicente; d. C. Lavorato.

Other specimens examined. *Otidea* aff. *subformicarum* — Mexico, Salazar, Parque Nacional Miguel Hidalgo, *Abies* forest, 23 Sept. 2007, *M. Hernández* (FH301035); Veracruz, Cofre de Perote, Camino de los Conejos, Los Lescados, montane forest of *Pinus teocote*, *P. montezumae*, *Arbutus jalapensis*, 18 Sept. 2007, *M.E. Smith* (FH301036).

Notes — *Otidea subformicarum* is closely related to *O. formicarum* based on both morphological and molecular characters. Both have broadly ear- to cup-shaped apothecia and small spores, and are associated with conifers. Diagnostic features of *O. subformicarum* are the orange-brown to reddish brown apothecial colours, and especially the long and narrow spores compared to related species. *Otidea formicarum* has shorter and comparatively more rounded spores (Fig. 20). All *O. subformicarum* apothecia were collected under *Pinus*, *Pseudotsuga menziesii* or *Abies*. The ecology of *O. formicarum* partly overlaps (see further under that species). *Otidea subformicarum* appears to have a southern European distribution, whereas *O. formicarum* is known only from Fennoscandia and the Alps. *Otidea subformicarum* forms a strongly supported clade in the ITS-LSU phylogeny (Fig. 2). The four ITS sequences of *O. subformicarum*, from Spain and Italy, are nearly identical (only S-F256979 differs in 1 bp), except for a small variation in the minisatellites. The ITS nucleotide diversity is 0.71 % in the four minisatellites unique to *O. subformicarum*. The five ITS sequences of *O. formicarum*, from Finland, Norway and Sweden, are likewise almost identical (only JS.08.63 differs in 2 bp). The ITS sequences of *O. subformicarum* and *O. formicarum* show many nucleotide differences (40 / 747 bp). Thus the interspecific ITS nucleotide diversity is much higher (5.35 %) than the intraspecific diversity (in *O. subformicarum* 0.07 % without the minisatellites and in *O. formicarum* 0.10 %).

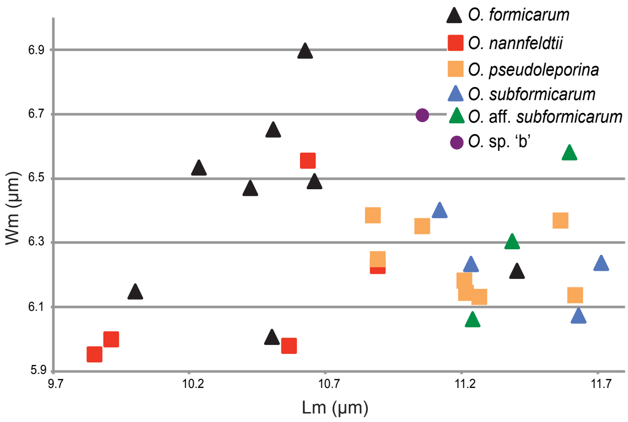

Fig. 20 Mean spore length and width in collections of species in the *O. formicarum* clade and *O. pseudoleporina*, based on 20 spores from each collection.

Two collections from Mexico, FH301035 and FH301036 (here referred to as *O.* aff. *subformicarum*), belong to the *O. formicarum* clade based on our molecular phylogenetic analyses (Fig. 1, 2). Although analyses of the combined ITS-LSU dataset did not resolve the relationships among these three lineages (Fig. 2) and the LSU phylogeny place FH301035 as a strongly supported sister taxon to two collections of *O. subformicarum*, our three- and four-gene phylogenies (Hansen & Olariaga 2015) suggest the two European species share a most recent common ancestor, and the Mexican collections diverged earlier. The spore size and shape of the Mexican collections conform to those of *O. subformicarum* (Fig. 20), but the apothecial colours differ in these collections. Fresh material has not been available to us, but the photo of fresh apothecia of FH301035 shows egg-yellow apothecia, clearly distinct from *O. subformicarum*. Photos of apothecia of FH301036 have a dark purplish brown colour, which has not been observed in *O. subformicarum*. Based on these colour differences and molecular characters, we suggest that those collections belong to an additional undescribed species, possibly endemic to North America. Further collections are needed to get insights into the variation and delimitation of this taxon for its formal description.

Outside the *O. formicarum* clade, a few species have similar spores to *O. subformicarum*. These differ by a combination of other features: *Otidea tuomikoskii* by narrowly ear-shaped apothecia, a receptacle surface with high warts (55–177 μm high), an ectal excipulum that turns yellow in KOH and typically orange ochre basal tomentum; and *O. nannfeldtii* by apothecia often having yellow tones, sometimes pink stains, and above all by the shorter spores (L_m = 10–10.7 μm).

Otidea unicisa **clade**

Apothecia with ochre yellow tones. Basal tomentum with ochre tones. Spores ellipsoid, with warts ± ridges or spinose. Resinous exudates on the outermost ectal excipulum cells dissolve and exude bright yellow pigment in KOH.

Species — *Otidea kaushalii*, *O. unicisa*, *O. yunnanensis.*

16. *Otidea kaushalii* (J. Moravec) K. Hansen & Olariaga, *comb. nov.* — MycoBank MB810994; Fig. 22

Basionym. *Sowerbyella kaushalii* J. Moravec, Mycol. Helv. 2: 94. 1986.

≡ *Aleurina kaushalii* (J. Moravec) W.Y. Zhuang & Korf, Mycotaxon 29: 312. 1987.

≡ *Otideopsis kaushalii* (J. Moravec) J. Moravec, Mycol. Helv. 3: 138. 1988.

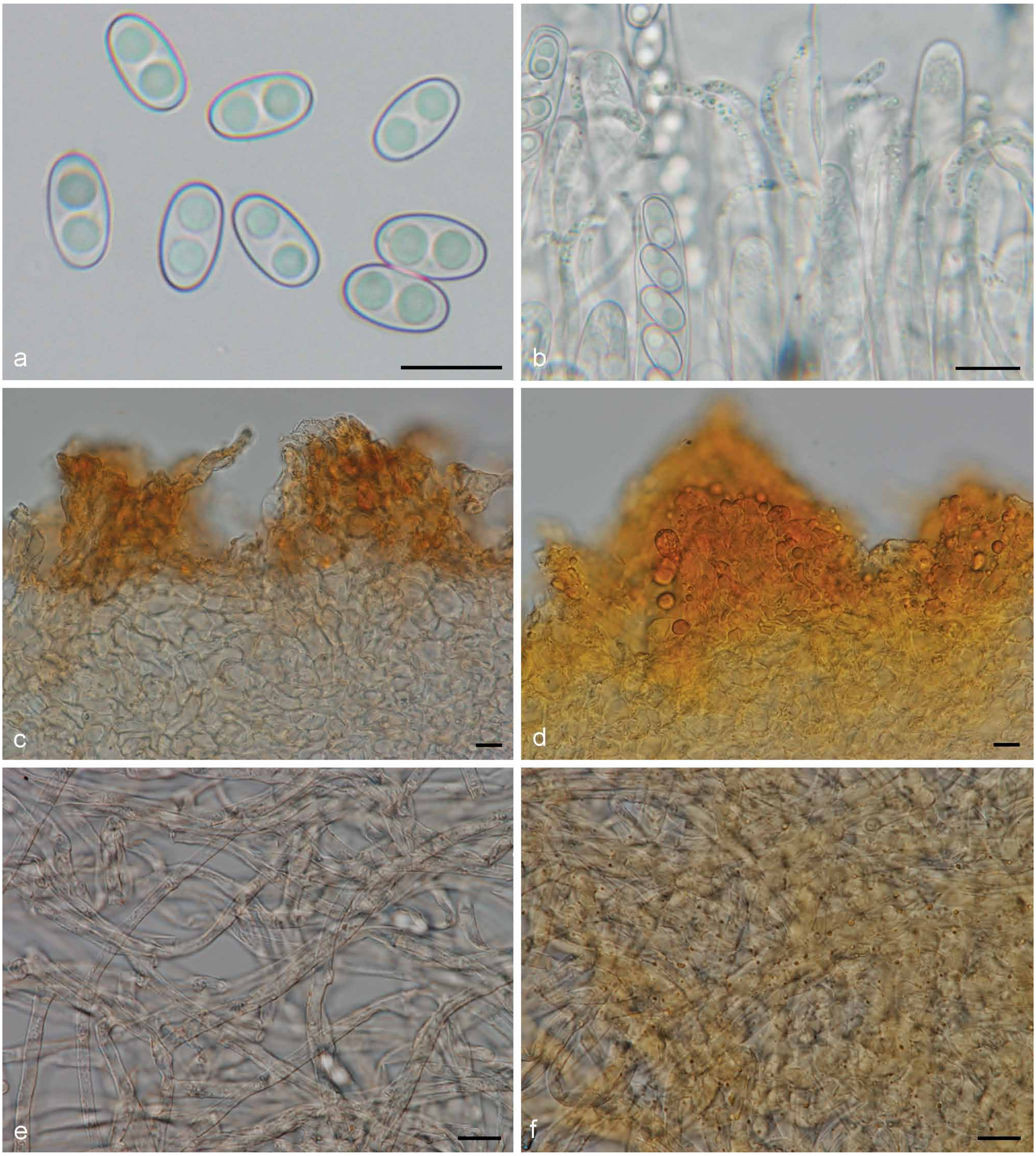

Fig. 21 *Otidea subformicarum* (S-F242696, holotype). a. Spores*; b. paraphyses and asci*; c. ectal excipulum in water showing reddish brown resinous exudates†; d. ectal excipulum in Melzer's reagent showing amber drops†; e. basal mycelium in water†; f. basal mycelium in Melzer's reagent†. — Scale bars = 10 μm; * = fresh material; † = dried material.

Holotype. India, West Bengal, Darjeeling, Batasi, on soil and decayed wood in angiosperm forest, alt. 7600 f, 6 Sept. 1979, *R. Kaushal*, PAN 18169. *Isotypes* herb. J. Moravec (CUP 61814, C-F-60847 !).

Apothecia 16–65 mm high, 12–62 mm wide, broadly ear-shaped, split, stipitate. *Hymenium* dirty grey to very faintly incarnate, greyish yellow, orange-ochre (5A6) when dried. *Receptacle surface* dark orange brown (6E7, 6E8) when dried, densely warty. Warts conical, acute or blunt, densely gregarious, darker than the background, dark reddish brown. *Stipe* 3–32 mm long, 3–10 mm wide. *Basal tomentum and mycelium* ochre (5A4). *Spores* ellipsoid to slightly subfusoid, inequilateral, with one or two large and/or a few small guttules, with thin, often curved, spines, up to 1(–1.5) µm high, denser at the poles, sometimes united in short ridges, hyaline, 14–17 × 7–9 µm (L_m = 14.9–15.7 µm, W_m = 7.7–7.9 µm, Q_m = 1.9–2; n = 2). *Paraphyses* curved to hooked, sometimes enlarged at apices, 2.5–5 µm wide, when dried containing small, yellowish refractive granules. *Apothecial section* 700–800 µm thick. *Asci* 188–213 × 11–13 µm. *Medullary excipulum* of *textura intricata*, hyphae thick-walled, hyaline to very pale yellow. *Ectal excipulum* of *textura globulosa-angularis*, 70–90 µm thick, of 3–4 cell layers, cells thin-walled, pale yellowish brown, 12–46 × 13–33 µm. Surface with conical warts, densely placed, 40–140 µm high, 50–137 µm wide, formed by globose to elongated cells, 8–11.5 µm broad. Resinous exudates abundant, reddish brown, amorphous, and/or many yellowish brown, crystal-like, oblate

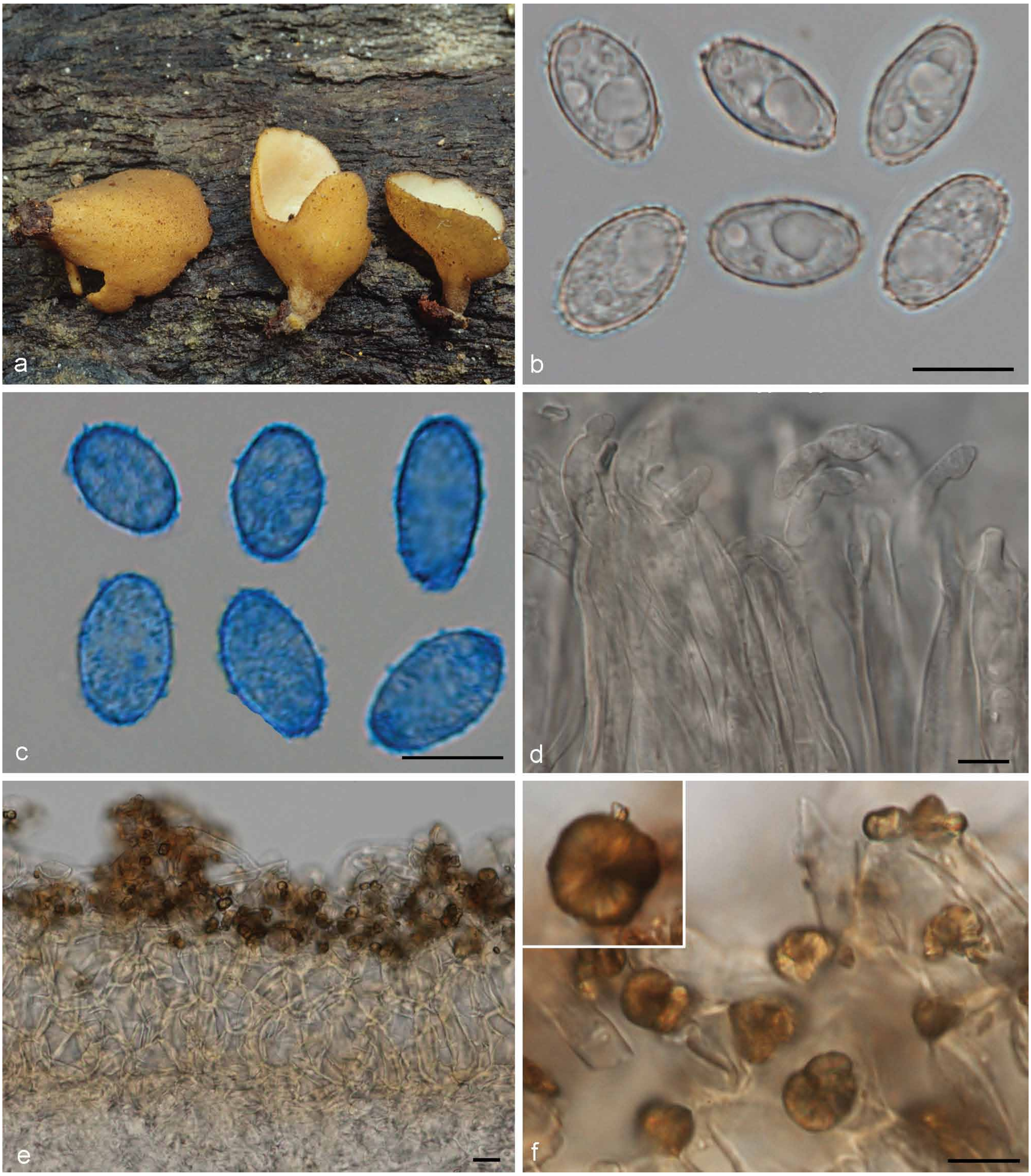

Fig. 22 *Otidea kaushalii*. a. Apothecia; b. spores in water†; c. spores in Cotton Blue†; d. paraphyses in KOH†; e. ectal excipulum and warts with abundant crystal-like, resinous exudates in water†; f. close-up of crystal-like, oblate spheroid exudates on outermost ectal excipulum cells in water† (a–d, insertion on f: T. Læssøe 6236; e, f: PAN 18169, isotype). — Scale bars = 10 µm; † = dried material. — Photos: a. T. Læssøe.

spheroid, 6–8 × 7.5–11 µm, striate bodies, with a constricted centre, not dissolving in MLZ, dissolving and exuding bright yellow pigment in KOH. *Basal mycelium* of 4.5–6 µm wide, thin-walled to slightly thick-walled, very pale yellow hyphae, unchanged in KOH, with regularly arranged, spheroid, yellow resinous exudates, dissolving in MLZ, unchanged in KOH.

Specimens examined. Malaysia, Sabah Kinabalu, on rotten wood, 2 Mar. 1999, *T. Læssøe* 6236 (C, dupl. BORH).

Notes — *Otidea kaushalii* is closely related to *O. yunnanensis* based on our analyses of the LSU (Fig. 1) and morphology. Already Moravec (1988) stated this, when he combined *O. kaushalii* in *Otideopsis*. The distinctly spiny spore ornamentation in these two species appears identical; see SEM photographs of the spores of the holotype of *O. kaushalii* in Moravec (1986) and of *O. yunnanensis* in Liu & Zhuang (2006). Both species have a receptacle surface with densely placed, high, dark brown warts and a lighter coloured hymenium, i.e. greyish yellow, cream to yellow. *Otidea kaushalii* is distinguished by the smaller spores, and possibly by the ectal excipulum of large, yellowish brown globose to angular cells (Fig. 22e). We report here for the first time a so far unique type of crystal-like, oblate spheroid, striate exudates on the outermost ectal excipulum cells of *O. kaushalii* (Fig. 22e, f) that might be confined to *O. kaushalii* within *Otidea*. These are abundant in both the isotype and the Malaysian material. A third collection of *O. kaushalii* has been reported by Zhuang & Korf (1987) from Xizang, China. The Malaysian and Chinese collections have smaller apothecia with shorter or almost no stipe (apothecia up to 19 × 18 mm; stipe 3 × 3 mm in the Malaysian material, Fig. 22a) as compared to

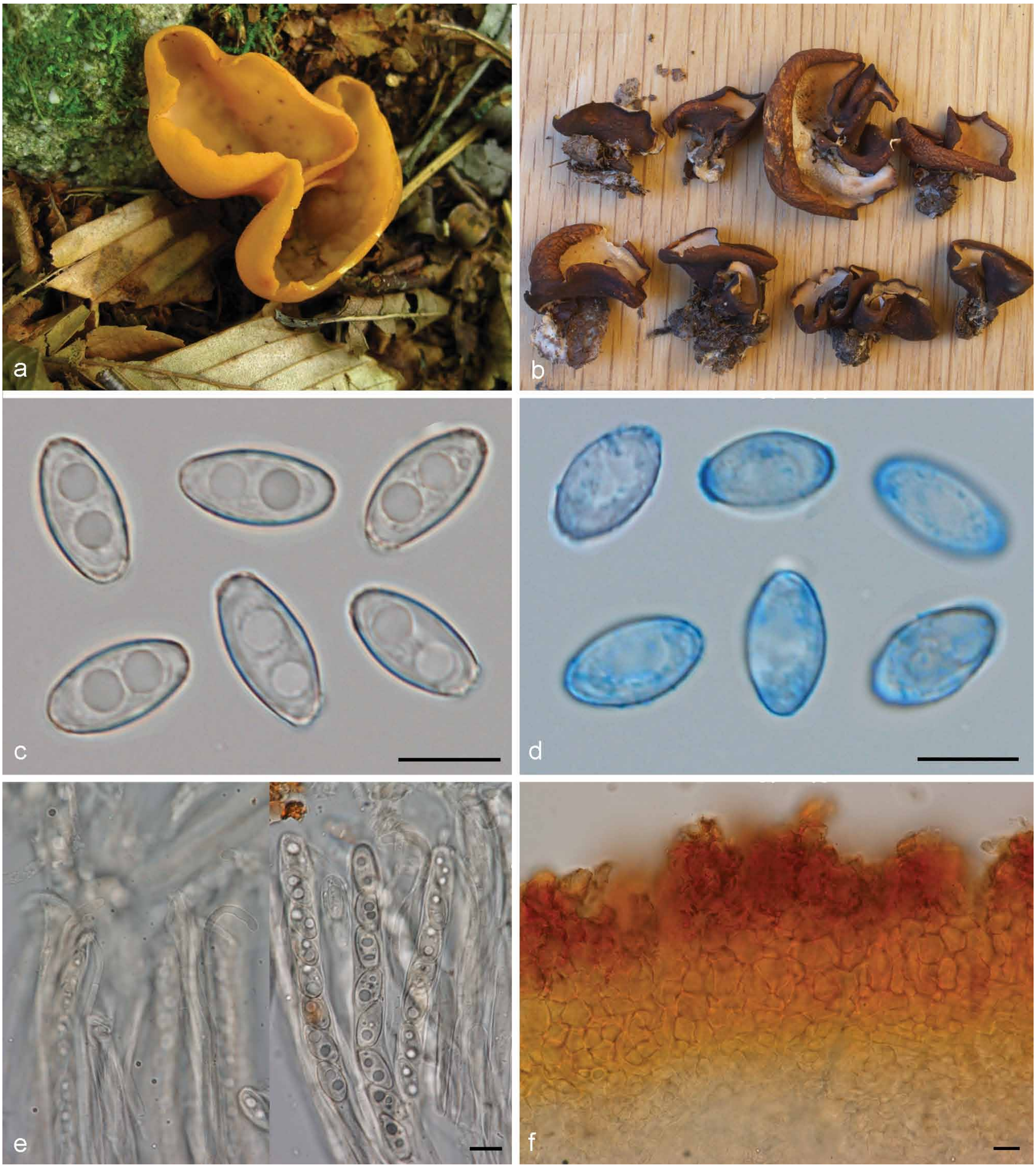

Fig. 23 *Otidea unicisa*. a. Apothecium; b. apothecia†; c. spores in water†; d. spores in Cotton Blue†; e. paraphyses in water†; f. ectal excipulum in water† (a: JK12082101; b: H7003343; c–f: KH.06.06). — Scale bars = 10 µm; † = dried material. — Photos: a. J. Karakehian.

the holotype (apothecia up to 65 × 62 mm; stipe 32 × 10 mm). The apothecia of *O. yunnanensis* have also been described with varying stipe length (6–25 × 4–6 mm).

17. ***Otidea unicisa*** (Peck) Harmaja, Karstenia 26: 44. 1986. — Fig. 23

Basionym. *Peziza unicisa* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 26: 81. 1874.

≡ *Sowerbyella unicisa* (Peck) J. Moravec, Czech Mycol. 47: 266. 1994.

Holotype. USA, New York, Lewis County, Croghan, Felt House, ground in woods, Sept. (NYSf 3283).

Misapplied names

– *Otidea grandis* sensu Kanouse, Mycologia 41: 672. 1949; Liu & Zhuang, Fung. Diversity 23: 188. 2006.

Apothecia gregarious to caespitose, 12–25 mm high, 12–35 mm wide, initially broadly ear-shaped, then becoming cup-shaped, split, stipitate or sessile. *Hymenium* ochraceous yellow, sometimes with pink tinges, yellowish ochre (5A5, 5B5), orange-ochre (5A6) when dried. *Receptacle surface* ochraceous yellow, when dried dark orange brown (6E7, 6F7), ochre-brown (5A4) towards the base, warty, occasionally with shallow ribs at the base. Warts rounded, gregarious, concolorous or slightly darker than the background, reddish brown. *Stipe* 4–8 × 2–4 mm. *Basal tomentum and mycelium* abundant, yellowish ochre (5A4). *Spores* ellipsoid to slightly fusoid, inequilateral, with two large guttules, often with a few smaller guttules, with small, low warts, often irregular ridges, denser at the poles, hyaline, (13–)14–15.5(–16.5) × 6.5–8.5 µm (L_m = 14.6–15.2 µm, W_m = 7.1–8 µm, Q_m = 1.8–2.1; n = 3). *Paraphyses* curved to hooked, sometimes enlarged at apices, 2.5–4 µm wide, sometimes with 1–2 low notches, when dried containing refractive, pale yellow granules. *Asci* 181–197 × 8–11 µm. *Apothecial section* 750–900 µm thick. *Subhymenium* c. 70–120 µm thick, of cylindrical cells, densely arranged. *Medullary excipulum* of *textura intricata*, 500–700 µm thick, hyphae thin-walled, 3.5–9 µm wide, hyaline to very pale yellow, without resinous exudates at septa. *Ectal excipulum* of *textura angularis*, 70–95 µm thick, cells thin-walled, hyaline to light yellow, 11–30 × 6.5–18 µm. Surface with conical warts, 35–85 µm high, formed by fasciculate, short, hyphoid hairs, of globose to elongated cells, constricted at septa, 6–11 µm wide. Resinous exudates abundant, dark yellowish to reddish brown, dissolving in part and converting into reddish particles in MLZ, turning brighter yellow in KOH. *Basal mycelium* of 4.5–6 µm wide, thin-walled to slightly thick-walled, hyaline to very pale yellow hyphae, unchanged in KOH, with regularly arranged, spheroid, yellow resinous exudates, dissolving in MLZ, unchanged in KOH.

Specimens examined. USA, Massachusetts, Carlisle, Great Farm, on woody debris, 8 July 2006, *L. Millman*, KH.06.06 (FH); Massachusetts, Carlisle, Towle Conservation Land, 15 July 2006, *L. Millman* (FH301030); Massachusetts, Purgatory Charm, 9 July 2003, *Z. Wang*, ZW Geo 65-Clark (S); Michigan, Cut R., Mackinac Co., in frondose woods, 10 Aug. 1949, *A.H. Smith* 33020 (UPS F-629380); Michigan, N of Hessel, Mackinac Co., in frondose woods, 15 Aug. 1949, *H. Imshaug* 3458 (UPS F-629377); Michigan, Luce Co., Tahquamenon Falls State Park, 21 Aug. 1951, *A.H. Smith* 39070 (UPS F-629382); Michigan, W of Detour on M134, Chippewa Co., in beech-maple woods, 14 Aug. 1949, *H. Imshaug* 3348 (UPS F-629379); New Hampshire, Shelburne (UPS F-629427); North Carolina, Macon Co., near summit of Standing Indian Mountain, on duff and buried wood of *Betula*, 1 Aug. 1969, *H.H. Burdsall* 2605 (dupl. H7003343); West Virginia, on light loam and leaf mold, 15 July 1896, *L.W. Nuttall*, Ellis 868 (UPS F-630023); West Virginia, Monongahela National Forest, Dolly Sods Wilderness, Wildlife Trail (TR 560), on soil among leaf litter under *Fagus grandifolia*, *Acer pennsylvanicum*, and *Betula* sp., 21 Aug. 2012, *J. Karakehian*, JK12082101 (FH, dupl. S).

Notes — *Otidea unicisa* is easily recognised by the spore ornamentation of low, delicate warts and short ridges. The dried specimens are typically bicoloured, with dark brown outside and orange-ochre hymenium. The spore ornamentation of *O. unicisa* was for a long time overlooked (Harmaja 1986). The ornamentation is clearly visible at 1 000×, especially at the poles where it is more prominent. We agree with Harmaja (2009a) that what Kanouse (1949) described under the name *O. grandis* is *O. unicisa*. The bicoloured apothecia with brown outside and orange hymenium, along with the ornamented spores, and spore sizes in the range of *O. unicisa*, support this view. Liu & Zhuang (2006) also gave a collection with the typical spore ornament of *O. unicisa* under the name *O. grandis* (for SEM of the ornament see their f. 8). Both studies mention the Boudier plate 328 (n°. 134, 1905; as *O. grandis*), which shows bicoloured apothecia. *Otidea unicisa* has not been recorded outside Eastern North America, and in our opinion the Boudier plate 328 shows typical *O. bufonia* apothecia. Corroborating this, two Boudier specimens labelled *O. grandis* (UPS F-629342 and likely the collection used for plate 328: PC0093644), studied by us, are in fact *O. bufonia*. For further comments on *O. grandis* see Excluded, dubious and imperfectly known taxa.

18. ***Otidea yunnanensis*** (B. Liu & J.Z. Cao) W.Y. Zhuang & C.Y. Liu, Fung. Diversity 23: 188. 2006

Basionym. *Otideopsis yunnanensis* B. Liu & J.Z. Cao, Shanxi Univ. J., Nat. Sci. Ed. 4: 70. 1987.

Holotype. CHINA, Yunnan, Dulong River, Lang Tuan, on ground in forest, 30 Aug. 1982, *D.C. Zhang* (HKAS 12150).

Otidea yunnanensis was described when the monotypic genus *Otideopsis* was erected. It was separated from *Otidea* because of the ornamented spores and paraphyses with fused apical portion (Liu & Cao 1987). Upon re-examination of the type material, Liu & Zhuang (2006) discovered that the paraphyses had free apices. They also concluded that the spores were with two large and several small guttules, and not multi-guttulate as originally described by Liu & Cao (1987). Our LSU phylogeny confirms that *O. yunnanensis* is deeply nested within *Otidea* (Fig. 1). The species is easily recognised within *Otidea* by the large spores with fine, curved spines. Different spore sizes have however, been reported from the holotype: 18–20 × 8–10 µm (including ornament, Liu & Cao 1987) and 15–21 × 9.7–10.5 µm (excluding ornament, Moravec 1988), and including one additional collection: 16.5–20 × 7.6–10 µm (Liu & Zhuang 2006). The very wide spore measurements given by Moravec overlap somewhat with the spore length of the closely related *O. kaushalii* (for further comparisons see under *O. kaushalii*).

Otidea bufonia-onotica **clade**

Apothecia dark brown or ochre yellow. Basal tomentum with brown or yellow tones, especially when dried. Spores fusoid or ellipsoid, smooth. Resinous exudates on the ectal excipulum converting into reddish particles or melting into amber drops.

Species — *Otidea brevispora*, *O. bufonia*, *O. fusconigra ad interim*, *O. mirabilis*, *O. onotica*, *O. purpurea*, *O. smithii.*

19. ***Otidea brevispora*** (W.Y. Zhuang) Olariaga & K. Hansen, *comb. & stat. nov*. — MycoBank MB808974

Basionym. *Otidea onotica* var. *brevispora* W.Y. Zhuang, Mycotaxon 94: 368. 2006 ‘2005’.

Holotype. CHINA, Yunnan, Baoshan, 24 July 2003, *Z.L. Yang* (HKAS 43003) !

Otidea onotica var. *brevispora* was distinguished from *O. onotica* based on shorter spores (Zhuang 2006). Our study of the *O. brevispora* holotype confirmed the smaller spores (9.5–10.5 × 5.5–6 µm; L_m = 9.9 µm, W_m = 5.6 µm, Q_m = 1.75). Otherwise *O. brevispora* shares all macro- and microscopic features with

O. onotica, including the yellow reaction of the basal mycelium in KOH. Our ML analyses, with an LSU GenBank sequence of the Chinese holotype, show *O. onotica* var. *brevispora* is a sister taxon to a clade of *O. onotica* specimens (Fig. 1). Based on this and the smaller spores we consider it to be a distinct species.

20. *Otidea bufonia* (Pers.) Boud., Hist. Classif. Discomyc. Europe: 52. 1907. — Fig. 4b, c, 5b, 24

Basionym. *Peziza bufonia* Pers., Mycol. Eur. 1: 225. 1822: Fr., Syst. Mycol. 2: 54. 1822.

≡ *Geopyxis bufonia* (Pers.) Sacc., Syll. Fung. 8: 73. 1889.

Lectotype designated here: France, in sylvula Vincennes, Aug. 1816 (L 0116690 / 911.81.97, Persoon herbarium) !; MycoBank MBT178089.

= *Peziza umbrina* Pers., Observ. Mycol. 2: 77. 1799.

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

≡ *Peziza cochleata* var. *umbrina* (Pers.) Fr., Syst. Mycol. 2: 50. 1822: Fr. loc. cit (‘α *umbrina*’).

≡ *Otidea umbrina* (Pers.) Bres., Fungi Trident. Ser. 2, fasc. 11–13: 68. 1898.

Lectotype designated here: Sowerby, Col. Fig. Engl. Fung. 1: t. 5. 1797 (as *Peziza cochleata*); MycoBank MBT200088.

= *Peziza pseudobadia* Cooke, Mycographia part 4: 176. 1877.

≡ *Aleuria pseudobadia* (Cooke) Gillet, Champ. France Discomycetes: 38. 1879 (‘*pseudo-badia*’).

≡ *Geopyxis pseudobadia* (Cooke) Sacc., Syll. Fung. 8: 69. 1889 (‘*pseudo-badia*’).

Holotype. France, Mérignac, sur un mur, 1814 (K(M) 195314, ex herb. Cooke).

= *Otidea pedunculata* Velen., Monogr. Discomyc. Bohemiae 1: 354. 1934.

Lectotype designated here: Czech Republic, Hrusice, Aug. 1924, *J. Velenovský* (PRM 147622) !; MycoBank MBT200086.

Fig. 24 *Otidea bufonia**. a, b. Apothecia; c. spores; d. paraphyses; e. ectal excipulum; f. basal mycelium (a: KH.09.172; b: JS.08.55; c–f: KH.09.171) — Scale bars = 10 µm; * = all fresh material. — Photos: b. J. Santos.

Misapplied names

– *Otidea grandis* sensu Boudier, Icon. Mycol. livr. 6: n°. 134, pl. 328. 1905 (preliminary text with ‘circulaires’).

– *Peziza cochleata* sensu Sowerby, Col. Fig. Engl. Fung.1: t. 5. 1797.

Apothecia gregarious, rarely caespitose, 15–45 mm high, 17–32 mm wide, initially ear-shaped, then soon expanding and becoming deeply cup-shaped, split, stipitate or sessile. *Hymenium* initially orange brown (6C6) sometimes olivaceous brown (4D6), then dark orange brown (6F6, 7E8), when dried greyish brown (5E3, 5E4), slightly purple. *Receptacle surface* dark brown (6E4–6E7), sometimes pale rusty brown (6D8, 6E8) or purplish brown (6E3) or with olivaceous tones, slightly hygrophanous, in drying slightly paler, when dried dark orange brown (6E5, 6F4), warty, seldom slightly wrinkled at the base. Warts conical to flattened, gregarious, dark brown, sometimes distinctly darker than the background. *Stipe* 5–14 × 7–10 mm, often hollow and felty inside. *Smell* weak; taste mild. *Basal tomentum and mycelium* abundant, brownish white to light brown (6B3). *Spores* narrowly fusoid, rarely ovoid, inequilateral, with two large guttules, very rarely with a third small guttule, smooth, hyaline to pale yellowish, (12–)13–16.5(–18) × 6–7.5(–8) µm (L_m = 12.4–16.1 µm, W_m = 6.3–7.3 µm, Q_m = 1.9–2.5; n = 8). *Paraphyses* hooked, a few curved, of the same width or slightly enlarged at apices, 3.5–5(–7) µm wide, without notches or rarely with a notch on the underside, when fresh containing small, refractive, light brownish yellow guttules; when dried light brownish yellow. *Asci* 143–172 × 10–12 µm. *Apothecial section* 1000–1300 µm thick. *Subhymenium* c. 70–100 µm thick, visible as a darker zone, composed of cylindrical to swollen cells, densely arranged, with scattered brownish resinous exudates at septa. *Medullary excipulum* of *textura intricata*, 500–700 µm thick, hyphae thick-walled, 3.5–9 µm wide, hyaline to light brown, some covered with strikingly dark brown, striate resinous exudates. Big crystal-like aggregates sometimes present among the hyphae, dissolving in KOH, visible in MLZ. *Ectal excipulum* of *textura angularis*, 80–100 µm thick, cells thin-walled, brownish, 16–31 × 11–25(–30) µm. Surface with broadly conical warts, 40–80 µm high, formed by short, fasiculate hyphoid hairs, of 3–4 subglobose to elongated cells, constricted at septa, 6–11 µm wide, sometimes with a gelatinous sheath. Resinous exudates abundant, dark brown, partly dissolving and converting into small reddish particles in MLZ, partly dissolving in KOH. *Basal mycelium* of 3.5–4.5 µm wide, hyaline to brown hyphae, with oily, light brown drops on the surface, sometimes crystalloid and rod-shaped.

Specimens examined. Czech Republic, Prague-East district, infra Klokočná, in carpineto, 5 Oct. 1931, *J. Velenovský* (PRM 150074, syntype of *O. pedunculata*). – Denmark, Fyn, Juelsberg Skov, N of Nyborg, along roadside in *Fagus* forest, 28 Sept. 1986, *D. Boertman* (C-F-47790); E Jylland, Løvenholm Skovene, Eldrup Skov, in grass along road, 23 Sept. 1979, *E. Andersen* (C-F-86688); E Jylland, Vejle Nørreskov, at roadside on rich soil under *Populus tremula*, *Alnus*, *Corylus*, *Betula*, *Fraxinus*, *Fagus*, etc., 13 Sept. 1993, *J. Vesterholt* (C-F-20453); NE Jylland, Rubjerg Knude, under *Abies*, 18 Sept. 1989, *C. Lange & J. Vesterholt* (C-F-25955); NW Jylland, Nystrup Plantage near Thisted, 1 Sept. 1972, *K. Toft* (C-F-48018); W Jylland, Bordrup Plantage, in *Picea* and *Pinus* plantation along forest road on sandy ground, 17 Sept. 2011, *M. Sasa* (C-F-94240); Lolland, Favrsted Skov, among mosses, on calcareous soil, by forest-road under *Fagus*, 4 Oct. 2007, *K. Hansen & B. Kullman*, KH.07.37 (S); Sjælland, Feldskoven near Sorø, 14 Aug. 1974, *M. Lange* (C-F-47995); N Sjælland, Gribskov, under *Fagus* in the forest, 19 Sept. 1971, *H. Dissing* (C-F-48019); ibid., 8 Oct. 1973, *P.M. Pedersen* (C-F-48015); Sjælland, Horserød Hegn, 6 km W of Helsingør, along roadside, 17 Sept. 1964, *H. Dissing* (C-F-48000). – Finland, Varsinais-suomi, Lohja, Virkkala, Pähkinäniemi, herb-rich deciduous forest on calcareous, mull soil, with *Corylus avellana*, *Betula pendula*, *Populus tremula*, *Picea abies* and *Pinus sylvestris*, 28 Aug. 1997, *J. Vauras* 12503F (TUR-A, dupl. S). – France, Fontainebleau, on the ground under *Quercus* and *Abies*, Oct. 1876, *E. Boudier* (PC0093644, as *O. grandis*); Forêt de Châtellerault (L 0111782, Herb. Persoon, as *Peziza umbrina*); Landes, Contis, under *Pinus pinaster* on sandy soil, 6 Dec. 2009, *J.L. Teres*, KH.09.249 (S); Loire-Atlantique, Bourgneuf-en-Retz, 5 Nov. 2009, *G. Moyne*, NV 2009.11.01 (S); Picardie, Compiègne, Oct. 1892, *E. Boudier* (UPS F-629342, as *O. grandis*); Saône-et-Loire, Robin, on the ground under *Corylus* and *Quercus*, *J.-P. Dechaume*, NV 2008.09.12 (dupl. S); Vendée, Jard-sur-Mer, in dune forest with dominance of *Pinus pinaster* and *Quercus ilex*, *G. Ouvrard*, NV 2006.11.07 (S); Vosges, Rambervillers, forêt de Saint-Hélène, under *Alnus* in a peatbog, 5 Oct. 2006, *M. Hurtu*, NV 2006.10.12 (S). – Italy, Caorle (VE), Brussa, Vallevecchia, under *Pinus pinea* close to the sea, 4 Nov. 2001, E. Campo (S-F257089); Ceva (CN), 9 km from the city on the road to Viola, on the side of a track under *Quercus pubescens*, *Castanea sativa* and *Corylus avellanea*, 16 Sept. 2005, *M. Carbone* (S-F257088); Deiva Marina (SP), under *Quercus ilex*, 5 Nov. 2008, *M. Carbone* (S-F257090); Piemonte, Vignole Borbera (AL), Fraz. Variano superiore, in soil under *Quercus pubescens* and *Castanea sativa*, 19 Oct. 2010, *M. Carbone* (S-F257087). – Spain, Barcelona, entre Sant Feliu de Codines y Castellterçol, forest with *Quercus ilex* and *Pinus sylvestris*, on calcareous ground, 14 Oct. 1976, *C. Montoliu* (AH44527); Huesca, Javierregay, under *Quercus rotundifolia* and *Q. humilis* humus, 5 Dec. 2009, *F. Prieto & A. González* s.n. (S); Navarre, Arbizu, in mixed forest, 14 Nov. 2009, *J. Martín* (ARAN-Fungi A5048005); Navarre, Etxauri mendatea, under *Quercus ilex*, 2 Dec. 2006, *J.M. Lekuona* (ARAN-Fungi A5053019); Navarre, Lete, under *Quercus faginea* and *Q. rotundifolia* on calcareous ground, 19 Dec. 2009, *J.L. Teres & P.M. Pasaban*, KH.09.248 (S); Valladolid, Tudela de Duero, Puente Hierro, under *Quercus ilex*, *J. Santos* (S-F22110). – Sweden, Gotland, near Visby, Värnhem, under *Fagus* and *Quercus robur* on rich ground, with *Hepatica nobilis*, 22 Sept. 2009, *E. Bohus-Jensen*, *K. Hansen & I. Olariaga*, KH.09.189 (S); Skåne, Degeberga, Mörkavad, broadleaf forest, 27 Sept. 2001, *S.-Å. Hanson*, SÅH 2001-253 (C); Skåne, Helsinborg, Gyhult, broadleaf forest dominated by *Fagus* and *Quercus*, on the ground, 13 Oct. 1994, *S.-Å. Hanson*, SÅH 16457 (C); Uppland, Stockholm, Enebyberg, Rinkebyskogen, on rich soil in deciduous forest, under *Corylus*, but also *Tilia*, *Quercus* and *Betula*, 1 Sept. 2008, *J. Santos*, JS.08.55 (S); ibid., 17 Sept. 2008, JS.08.79 (S); Uppland, Uppsala, Hågadalen-Nåsten Nature Reserve, Predikstolen, under *Quercus robur*, *Picea abies*, *Corylus* and *Salix*, on rich bare ground, 17 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.171 (S); ibid., KH.09.172 (S); Uppland, Vaksala, near Törnby, Ekbacken, grassy ground with bare patches of soil, close to a *Quercus robur* tree, 13 Sept. 2010, *K. Gillen & I. Olariaga*, KH.10.199 (S); Öland, Algustrum, Hönstorp, 500 m SO of the village, grazed mixed deciduous forest, 19 Sept. 1993, *T. Knutsson*, TK93-209 (S); Öland, Långlöt, Åstad, c. 75 m from Björkerumsvägen, c. 550 S of the T-crossing in Åstad, under *Corylus*, 6 Sept. 1998, *T. Knutsson*, TK98-208 (S). – USA, Michigan, Cheboybogan Co., Colonial Pt, Burt L., in beech-maple woods, 9 Aug. 1951, *A.H. Smith* 37560 (UPS F-629510); Michigan, Emmet Co., Pellston, in beech-maple woods, 11 Aug. 1951, *A.H. Smith* 37654 (UPS F-629511); Minnesota, Itasca State Park, on soil in mesic deciduous woods of red oak, bur oak, birch, hazelnut, *Ostrya*, 28 July 2010, *R.A. Healy*, RH1218 (MIN 933332); Minnesota, Lake Alexander SNA, on soil in mixed woods with canopy or red oak, *Ostrya*, white birch, 16 Aug. 2011, *R.A. Healy*, RH1393 (MIN 9333323). – Without locality (L 0111780, Herb. Persoon, as *Peziza umbrina*); (L 0111781, Herb. Persoon, as *Peziza umbrina*).

Notes — *Otidea bufonia* is macroscopically characterised by the cup-shaped apothecia, with a dark brown outside and a brown basal tomentum, especially in dried specimens. Microscopically, the narrowly fusoid spores and the presence of hyphae with striate resinous exudates in the medullary excipulum are important diagnostic characters. *Otidea mirabilis* is very similar to *O. bufonia* (see under *O. mirabilis*).

The hymenium colour shows a high variability in *O. bufonia* (Fig. 24a, b); we have observed orange brown, olivaceous or dark brown tones within a single collection. Also the colour of the receptacle surface varies and can be with rusty to purplish brown or olivaceous tones. If purplish tones are present it may be confused with *O. mirabilis*. The pigmented, striate, crystal-like exudates on the hyphae of the medullary excipulum are considered a unique feature for *O. bufonia* (Korf & Zhuang 1991, Harmaja 2009a, Parslow & Spooner 2013), and have been used to separate *O. bufonia* from *O. mirabilis* (Carbone et al. 2010, Van Vooren 2010). Our results strengthen this view. We have observed striate exudates in all the material examined (Fig. 4b, c). The size and abundance of the striate exudates are variable, and often restricted to the outermost part of the medullary excipulum (Fig. 4b). In *O. mirabilis* we have only observed biflabellate, crystal-like exudates (Fig. 4d).

An exceptional *O. bufonia* specimen with deviant spore characters was discovered (NV 2009.11.01), in which the spores were ovoid and considerably shorter than in the rest of the material. This collection is nested within the *O. bufonia* clade, along with typical collections.

Nomenclatural notes — A specimen from the Persoon herbarium (911.81.97, L0116690) labelled as *O. bufonia* by Persoon can be considered type material (Harmaja 2009a, b), being collected prior to the publication of *O. bufonia*. We designate it here as the lectotype to stabilise the name. It includes a single dark brown apothecium, with uniseriate, smooth, subfusoid spores, 14–16 × 5.8–7 µm, curved paraphyses, numerous dark brown, striate exudates on the hyphae of the medullary excipulum, and outermost ectal excipular cells with dark brown resinous exudates.

Otidea umbrina has been recognised as a separate species (Medardi 1995, Dissing 2000), based mainly on different hymenium colour. The original description of *O. umbrina* and the Sowerby plate to which Persoon (1799) referred, agree with our concept of *O. bufonia*. Confirming Harmaja (2009a), three of the four collections of *O. umbrina* studied by us and kept in Persoon´s herbarium in L belong to *O. bufonia*. Thus we regard *O. umbrina* as a synonym of *O. bufonia* in accordance with other authors (Dennis 1978). The name *O. bufonia* is sanctioned at specific rank and thus has priority over *O. umbrina*, which is sanctioned only at variety rank. The name *O. grandis* has been used for *O. bufonia* collections with bicoloured hymenium, i.e.

Fig. 25 *Otidea mirabilis**. a, b. Apothecia; c. spores; d. paraphyses; e. ectal excipulum; f. ectal excipulum wart in Melzer’s reagent, showing reddish reaction of resinous exudates (a: KH.09.188; b: KH.10.294; c–f: KH.10.308). — Scale bars = 10 µm; * = all fresh material.

orange-brown or olivaceous hymenium in contrast to a dark brown outside (Boudier 1905, Van Vooren 2010). For the interpretation of *O. grandis* see Excluded, dubious and imperfectly known taxa. We synonymise *O. pedunculata* with *O. bufonia* based on the study of two syntypes, and lectotypify it with PRM 147622. The lectotype shows dark brown, split apothecia, fusoid spores (13.5–15.5 × 5.5–6.5 µm, from 8 spores) and importantly striate exudates on some of the hyphae of the medullary excipulum. Harmaja (2009b) studied the holotype of *P. pseudobadia* and found it is a later synonym of *O. bufonia*. Only one collection of *P. pseudobadia* could be located in Kew (K(M) 195314); it is from Mérignac as given in the protologue, but from a wall, whereas Cooke wrote 'on the ground'. In any case, one of the apothecia corresponds well to the illustration in the protologue, and we consider this the holotype (and the material studied by Harmaja, although no annotation by him could be found; pers. comm. B. Aguirre-Hudson).

21. **Otidea mirabilis** Bolognini & Jamoni in Jamoni, Funghi e Ambiente 85–86: 56. 2001. — Fig. 4d, 25

Holotype. Italy, Piemonte, Alagna valsesia (VC), Val d'Otro, on soil under *Picea* and *Larix*, alt. c. 1500 m, 3 Sept. 1999, *D. Bolognini*, GMFN 1951. *Isotype* (S-F256929) !

Misapplied names
– *Otidea leporina* sensu Zhuang pro parte, Mycotaxon 96: 367. 2005.

Apothecia gregarious or caespitose, 18–62 mm high, 9–52 mm wide, initially ear-shaped, short or elongated, soon expanding and becoming deeply cup-shaped, split, stipitate or sessile. *Hymenium* initially reddish ochre (5B7, 6B7) or sometimes olivaceous brown (5F5, 5F6), then dark reddish ochraceous brown (5D8) to dark purple brown (6F4–6F7), when dried ochraceous brown (5D6) to purplish brown (6E5, 6E6). *Receptacle surface* dark purple brown with bluish lilaceous shades (7F2, 7F3), fading away with time to ochraceous dark-brown (5D7), then dark purple brown (6F4–6F7), sometimes with greyish ochre (4A3, 4B3) patches in unexposed parts, hygrophanous, in drying light purple brown (5D2, 6D2) to ochre brown (5B4), when dried purple brown (6D4, 6F3, 6F4), warty, often wrinkled at the base. Warts broadly conical to hemispherical, obtuse, gregarious, dark brown, sometimes distinctly darker than the background. *Stipe* 7–17 × 3–7 mm. *Smell* weak, vaguely resin-like; taste mild, slightly bitter in the end. *Basal tomentum and mycelium* abundant, whitish to light brown (5A3). *Spores* narrowly fusoid, inequilateral, with two large guttules, very rarely with additional 1–3 small guttules, smooth, hyaline to pale yellowish, (13–)13.5–16(–17) × 6–7(–7.5) µm (L_m = 14.1–15.4 µm, W_m = 6.3–6.9 µm, Q_m = 2.1–2.3; n = 9). *Paraphyses* curved to hooked, of the same width to slightly enlarged at apices, 2.5–5 µm wide, without or occasionally with a few low notches towards the apex, when fresh containing small, refractive, light brownish yellow guttules; when dried refractive, hyaline guttules. *Asci* 178–204 × 9–11 µm. *Apothecial section* 1000–1300 µm thick. *Subhymenium* c. 100–150 µm thick, visible as a darker zone, composed of irregularly, densely arranged, globose cells, with scattered brownish resinous exudates at septa. *Medullary excipulum* of *textura intricata*, 600–900 µm thick, hyphae 4–11(–15) µm wide, sometimes slightly swollen, thin to thick-walled, hyaline to light brown, seldom with brown resinous exudates at septa or biflabellate exudates, sometimes forming cross-like aggregates. *Ectal excipulum* of *textura angularis*, 80–100 µm thick, cells thin-walled to slightly thick-walled, brownish, 8–30 × 8–18 µm. Surface with broadly conical warts, 35–55 µm high, formed by short, fasciculate, hyphoid hairs, of 2–4 subglobose to elongated cells, constricted at septa, 6.5–10(–17) µm wide, sometimes with a gelatinous sheath. Resinous exudates abundant, dark brown, partially dissolving and turning reddish in MLZ. *Basal mycelium* of 3–6 µm wide, light yellow to light brown hyphae, seldom with oily brownish drops on the surface, with abundant small dark brown resinous exudates, rounded to irregular.

Specimens examined. Denmark, Bornholm, Rø Plantage, on needle layer under *Picea*, 30 Sept. 2001, *C. Lange*, KH.01.09 (C). – Finland, Koillismaa, Kuusamo, Oulanka National Park, Ampumavaara, south of the main road to Liikanen, 14 Aug. 2010, *M. Carbone* (S-F257083). – France, Isère, Lans-en-Vercors, 1300 m, on the ground, on litter, under *Larix*, 20 Sept. 2008, *J. Cavet*, NV 2008.09.14 (dupl. S). – India, Uttarakhand, Kalika, Nainital, on loose humus soil, 22 Sept. 1973, *S. Chandes* (UPS F-630072). – Italy, Friuli Venezia Giulia, Tarvisio (UD), Val Saisera-Valbruna, on calcareous soil under *Picea abies*, *Larix decidua* and *Fagus sylvatica*, 27 Sept. 2010, *G. Dose* (S-F257092). – Norway, Rana, St. Alteren, 7 km W of Mo i Rana, 4 Sept. 1972, *H. Dissing* (C-F-87187). – Sweden, Gotland, Ala, Näsmyr, under *Picea* and *Pinus sylvestris* on calcareous ground, 30 Sept. 2010, *E. Bohus-Jensen*, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.294 (S); Gotland, Ljugarn, forest close to Kaupungs Fridhem, under *Picea abies* on calcareous ground, under a cliff, 27 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.279 (S); Gotland, Lojsta hed, Russpark, grazed forest with *Pinus sylvestris*, on calcareous ground, 2 Oct. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.308 (S); Gotland, near Visby, Rävhagen, under *Pinus sylvestris*, with small *Quercus robur*, *Helianthemum* sp., *Melampyrum pratense*, *Gallium verum*, on sandy and acidified soil, 22 Sept. 2009, *E. Bohus-Jensen*, *K. Hansen & I. Olariaga*, KH.09.188 (S); Gotland, Tofta, Smågårde naturskog Nature Reserve, Tofta strand, under *Pinus sylvestris* on calcareous ground, 28 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.285 (S); ibid., KH.10.288 (S).

Otidea cf. *mirabilis* — Sweden, Öland, Gräsgård, Solberga, Stora Alvaret, 1300 m S of the village, 17 Oct. 1993, *T. Knutsson*, TK93-276 (S).

Notes — *Otidea mirabilis* is characterised by dark brown apothecia, purple to lilaceous-bluish shades in the receptacle surface of especially young apothecia, fusoid spores, and when present, biflabellate, crystal-like exudates in the medullary excipulum. *Otidea mirabilis* and *O. bufonia* are strongly supported as sister species in our multigene phylogeny (Hansen & Olariaga 2015). Thorough morphological comparisons show that *O. bufonia* differs from *O. mirabilis* in lacking lilaceous-bluish shades, and having brown striate exudates on some hyphae of the medullary excipulum. *Otidea smithii* is distinguished from *O. mirabilis* by the shorter spores with lower Q_m (1.9–2.0).

Otidea mirabilis was described with emphasis on the lilaceous tones of the outside, in contrast to the paler ochre to olivaceous hymenium (Jamoni 2001). Part of our material shows this colour pattern, but collections with dark brown hymenium have also been observed. Some authors have noted the absence of pigmented resinous exudates in the medullary excipulum of *O. mirabilis* (Carbone et al. 2010, Van Vooren 2010). We have, however, observed brown crystal-like exudates in KH.10.308 and the holotype. They are flabellate and forming cross-like aggregates (Fig. 4d), clearly different from those present in *O. bufonia* (Fig. 4b, c).

Coniferous forests on calcareous ground are the typical habitat of *O. mirabilis*. Two Chinese collections assigned to *O. leporina* by Zhuang (2006) and sequenced by Liu & Zhuang (2006) are resolved in the *O. mirabilis* clade in our LSU tree (Fig. 1). Based on morphology we report it also from India (UPS F-630072).

22. **Otidea onotica** (Pers.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 330. 1870. — Fig. 26

Basionym. *Peziza onotica* Pers., Syn. Meth. Fung.: 637. 1801: Fr., Syst. Mycol. 2: 48. 1822.

≡ *Scodellina onotica* (Pers.) Gray, Nat. Arr. Brit. Pl. 1: 668. 1821.

≡ *Peziza leporina* var. *onotica* (Pers.) P. Karst., Bidrag Kannedom Finlands Natur Folk 19: 41. 1871 ('*P. leporina* * *P. onotica*').

Lectotype designated here: Sowerby, Col. Fig. Engl. Fung. 1: t. 79. 1797 (as *Peziza leporina*). *Epitype* designated here: Sweden, Gotland, Ollajvs Nature Reserve, close to Ljugarn, calcareous ground in mossy *Picea* forest, 27 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.284 (S); MycoBank MBT178083.

= *Peziza rosea* Schumach., Enum. Pl. 2: 416. 1803.

Misapplied names

– *Otidea concinna* sensu Boudier, Icon. Mycol. livr. 26: n°. 552, pl. 325. 1909 (preliminary text with 'circulaires').

– *Peziza leporina* sensu Sowerby, Col. Fig. Engl. Fung.1: t. 79. 1797.

Apothecia gregarious to caespitose, 25–100 mm high, 14–80 mm wide, initially long and narrowly ear-shaped, then soon expanding, and becoming deeply cup-shaped, split, stipitate or sessile. *Hymenium* initially light yellow (4A3–4A5), then ochraceous yellow (4A6, 4A7, 5A6, 5A7, 5B6, 5B7), in some parts light orange (5A3, 5A4), often with pink tones or entirely pinkish (6A4), sometimes with red dots, when dried orange-ochre (5A5, 5A6) to reddish ochre (6B7, 6B8). *Receptacle surface* ochraceous yellow (4A6, 4A7), slightly hygrophanous, in drying slightly paler, when bruised sometimes brownish ochre (5B7) in the margin, when dried brownish ochre with orange tinge (5B7, 5B8), slightly warty, sometimes wrinkled at the base when old. Warts broadly conical, gregarious, concolorous or sometimes distinctly darker than the background, brown. *Stipe* 13–27 × 4–14 mm. *Smell* weak; taste mild. *Basal tomentum and mycelium* abundant, whitish to light yellow (4A2, 5A2). *Spores* ellipsoid to broadly ellipsoid, inequilateral, with two large guttules, smooth, hyaline, (11–)12–13.5(–14) × (5.5–)6–7 µm (L_m = 12.1–13.3 µm, W_m = 6.2–6.8 µm, Q_m = 1.8–2; n = 10). *Paraphyses* curved to hooked, of the same width or slightly broader at apices, 2.5–4.5 µm wide, without notches or rarely with a slightly swollen area on the underside, when fresh containing small, refractive, light yellow guttules; when dried hyaline to pale yellow guttules. *Asci* 138–233 × 9.5–12 µm. *Apothecial section* 850–1400 µm thick. *Subhymenium* c. 100–120 µm thick, of dense *textura intricata*, visible as a darker zone, cells

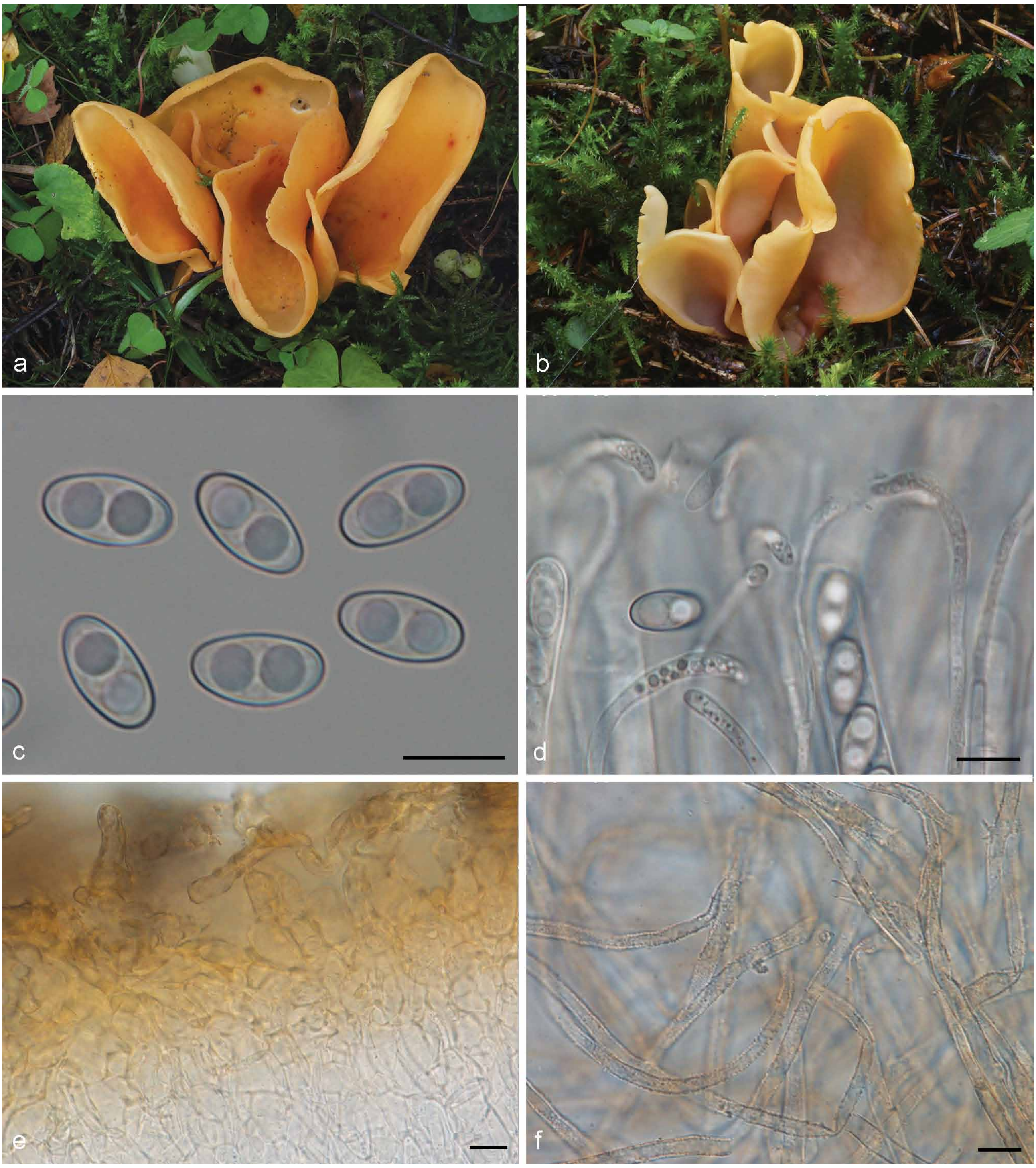

Fig. 26 *Otidea onotica**. a, b. Apothecia; c. spores; d. paraphyses; e. ectal excipulum; f. basal mycelium (a: KH.10.284, epitype; b: KH.09.132; c–f: KH.09.165). — Scale bars = 10 µm; * = all fresh material.

cylindrical to swollen, densely arranged. *Medullary excipulum* of *textura intricata*, 400–600 µm thick, hyphae 5–7(–12) µm wide, thick-walled, hyaline. *Ectal excipulum* of *textura angularis*, 80–110 µm thick, cells 13–55 × 11–28 µm, thin-walled, light yellow. Surface with conical warts, 85–105 µm high, formed by short, fasciculate hyphoid hairs, of 2–3 subglobose to elongated cells, constricted at septa, 11–14 µm wide. Resinous exudates abundant, yellow, dissolving into amber drops in MLZ. *Basal mycelium* of 3.5–6 µm wide, hyaline to very light yellow hyphae, turning yellow in KOH, with very small, regularly arranged, spheroid, resinous exudates on the surface, dissolving in MLZ, partially and more slowly in KOH.

Specimens examined. Czech Republic, South Bohemia, Netolice, Sept. 1922, *Hampl* (PRM 148341). – Denmark, Amager, Kongelunden, soil along forest path, 21 July 1998, *K. Hansen*, *T. Læssøe & C. Lange*, KH.98.107 (C); Møn, Fanefjord Skov, under conifers on calcareous influenced soil, 30 Sept. 2008, *H. Knudsen* (C-F-89691); Sjælland, Geelskov, 12 km N of Copenhagen, under *Fagus*, 18 Sept. 1963, *L. Hansen & A. Kjøller* (C-F-47985). – France, Landes, Contis phare, under *Pinus pinaster* on sandy soil, 9 Sept. 2009, *J.L. Teres* (ARAN-Fungi A8200131C). – Italy, Piemonte, Vinadio (CN), San Bernolfo, *Picea abies* and *Abies alba* forest, with presence of *Fagus sylvatica*, 29 Sept. 2008, *M. Carbone* (MCVE 23277). – Norway, Nord-Trøndelag, Gjøråsvika, Leksvik, under *Picea* on rich ground, among mosses, 3 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.132 (S); under *Corylus* and *Picea* on rich ground, KH.09.136 (S). – Spain, Gipuzkoa, Aia, Amezketalardiko bidegurutzea, under *Abies alba*, 3 Oct. 2009, *J.L. Teres* (ARAN-Fungi A3033701A); Madrid, Sierra de Guadarrama, deciduous forest, among *Quercus pyrenaica* leaves, 4 Oct. 1981, *G. Moreno* (AH2528); Navarre, Arbizu, mixed forest, 14 Nov. 2009, *J. Martín* (ARAN-Fungi A5048003); Navarre, Orokieta, Loiandi, in *Picea abies* plantation, 10 Oct. 2009, *Aranzadi ZE* (ARAN-Fungi A5041174-2). – Sweden, Skåne, Vittskövle, Segesholm, Herremöllan, broadleaf forest, 27 Sept. 2001, *S.-Å. Hanson*, SÅH 2001-266 (C); Uppland, Stockholm, Norra Järvafältet, Hansta Nature Reserve, on rich ground under *Picea abies* with *Corylus avellana*, 15 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.164 (S); ibid., KH.09.165 (S), KH.09.166 (S); Uppland, Uppsala, forest-covered hill NNE of Naturicum, coniferous forest with *Quercus* and *Corylus*, 4 Oct. 2011, *R. Sundin*, KH.11.108 (S); Uppland, Uppsala, Norra Lunsen Nature Reserve, Lunsentorpet, on rich organic soil, under dead standing *Picea*, 28 Aug. 2008, *J. Santos*, JS.08.48 (S); Uppland, Uppsala, Vänge, Fiby urskog Nature Reserve, old *Picea* forest, in the middle of a path, 17 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.175 (S). – USA, Minnesota, Cedar Creek ESR, on sandy soil in oak savannah, canopy of pin oak, hazelnut, 18 July 2011, *R.A. Healy*, RH1121 (MIN 933307); Minnesota, Lake Alexander SNA, on soil, mixed woods, canopy of red oak, paper birch, *Ostrya*, 29 July 2010, *R.A. Healy*, RH1222 (MIN 933311); Minnesota, Wild River State Park Many, on moist, sandy soil in mesic deciduous woods with oak, 23 July 2010, *R.A. Healy*, RH1199 (MIN 933309); Oregon, Benton Co., Philomath, Wood Creek Road, 18 Nov. 1996, *E.T. Peterson* (OSC 56759); Washington, Lower Tahoma Creek, Mt Rainier National Park, 27 Aug. 1948, *A.H. Smith* 30764 (UPS F-629424); Washington, Nisqually R., Mt Rainier National Park, 30 Aug. 1948, *H.A. Imshaug* 2116 (UPS F-629438).

Notes — *Otidea onotica* is one of the most common and well-known species of the genus. It is characterised by rather large, ochraceous yellow apothecia, often with a pinkish tinge, dots or stains in the hymenium, and spores of unusual size within *Otidea*. The presence of pinkish tones varies considerably. Apothecia ranging from entirely pink to completely devoid of pinkish tones have been observed in the same locality, in KH.09.132 and KH.09.136, respectively. These two collections have identical ITS sequences (GenBank accessions KM010103 and JN942772). A consistent character, here reported for the first time, is the yellow reaction of the basal mycelium in KOH. *Otidea unicisa* resembles *O. onotica* macroscopically, but is distinguished by ornamented spores.

Nomenclatural notes — Carbone (2009) revised the nomenclature of *O. onotica*. He considered the plate by Sowerby (1797, as *Peziza leporina*) the only element seen by Persoon, and thus, the holotype. However, Persoon did indirectly refer to two elements by giving the habitat in the protologue as beech forests (*faginetis*) and citing Sowerby's plate, which shows an oak leaf. Thus, the plate is not the holotype; i.e. the one element on which the author based the name (Art. 9.1 ICN; McNeill et al. 2012). The use of the term holotype could be corrected to lectotype according to Art. 9.9, but this article is not applicable since Carbone's holotype indication does not fulfil Art. 7.10 of the ICN (it does not include the phrase 'designated here' or equivalent) (McNeill et al. 2012). Carbone (2009) selected in addition an epitype from Persoon´s herbarium. But as an epitype must refer to the type it interprets and there was no validly selected type in 2009, the epitypification by Carbone is also not valid. We therefore typify *O. onotica* here, by designating as lectotype the Sowerby plate, supported by a newly collected epitype with multiple gene sequences and colour photographs. The selection of an epitype from Sweden is justified by the name being sanctioned (Fries saw and studied living material as indicated by '*v. v.*'), and our ITS sequences of *O. onotica* (4, 5, 6, 7, 8, 9) from Denmark, Italy, Norway and Sweden (including the epitype) being identical. The LSU sequences of *O. onotica* (4, 5) from Denmark and Sweden differ only 2 bp from the other collections.

23. ***Otidea purpurea*** (M. Zang) Korf & W.Y. Zhuang, Mycotaxon 22: 507. 1985

Basionym. *Acetabula purpurea* M. Zang, Acta Bot. Yunnan. 1: 101. 1979.
Holotype. China, Tibet, Zayu, on the ground in forest with *Pinus yunnanensis*, 1 Sept. 1976, *M. Zang* 670 (HKAS 5670) !

Notes — *Otidea purpurea* is probably closely related to *O. mirabilis.* It is also characterised by dark brown apothecia with lilaceous tones, but it clearly differs in the smaller spores (8.8–10 × 4.5–5.2 µm). Two additional taxa, *O. subpurpurea* and *O. bicolor*, should be compared with *O. purpurea*. *Otidea subpurpurea* likewise has violaceous tones on the outside, but has larger spores and asci (Zhuang & Yang 2008). *Otidea bicolor* has dark brown apothecia and small spores (Zhuang 2010), and is probably also closely related or conspecific with *O. purpurea*, based on the spore size. We treat here *O. purpurea* in the *O. bufonia* clade, because of the dark brown apothecia and brown basal tomentum.

24. ***Otidea smithii*** Kanouse, Pap. Michigan Acad. Sci., Part 1. 24: 28. 1939 '1938' — Fig. 27

Holotype. USA, California, Crescent City, 18 Nov. 1937, *A.H. Smith* 8843 (MICH 14408) !

Apothecia gregarious or caespitose, 32–70 mm high, 13–40 mm wide, initially narrowly ear-shaped, short or elongated, finally expanding, at late stages becoming deeply cup-shaped, split, normally shortly stipitate. *Hymenium* purple-brown (6D5) to dark purple-brown (7E5), then ochraceous brown (5D8), when dried very pale purplish brown (5A2). *Receptacle surface* dark purple-brown (7E5), sometimes with lilaceous shades or lighter ochre-brown (6C5) patches in unexposed parts, slightly hygrophanous, in drying dark ochraceous brown (6D7), when dried reddish brown (6E5, 6E6), warty, sometimes wrinkled at the base. Warts conical, obtuse or acute, gregarious, dark brown, sometimes slightly darker than the background. *Stipe* 12–26 × 5–12 mm. *Basal tomentum and mycelium* abundant, whitish to brown (5B2, 5C2). *Spores* ellipsoid, sometimes fusoid, inequilateral, with two large guttules, smooth, hyaline, 12–14(–14.5) × 6–7.5 µm (L_m = 12.5–13.6 µm, W_m = 6.4–7.1 µm, Q_m = 1.9–2.0; n = 5). *Paraphyses* curved to hooked, of the same width to slightly enlarged at apices, 3–5 µm wide, sometimes with 1–3 notches or with a low notch near the apex, when dried containing refractive, pale yellow guttules. *Asci* 175–251 × 9–11 µm. *Apothecial section* 800–1300 µm thick. *Subhymenium* c. 140–180 µm thick, of dense *textura intricata*, visible as a darker zone, hyphae intermixed with a few subglobose cells, with scattered brownish resinous exudates at septa. *Medullary excipulum* of *textura intricata*, 700–950 µm thick, hyphae

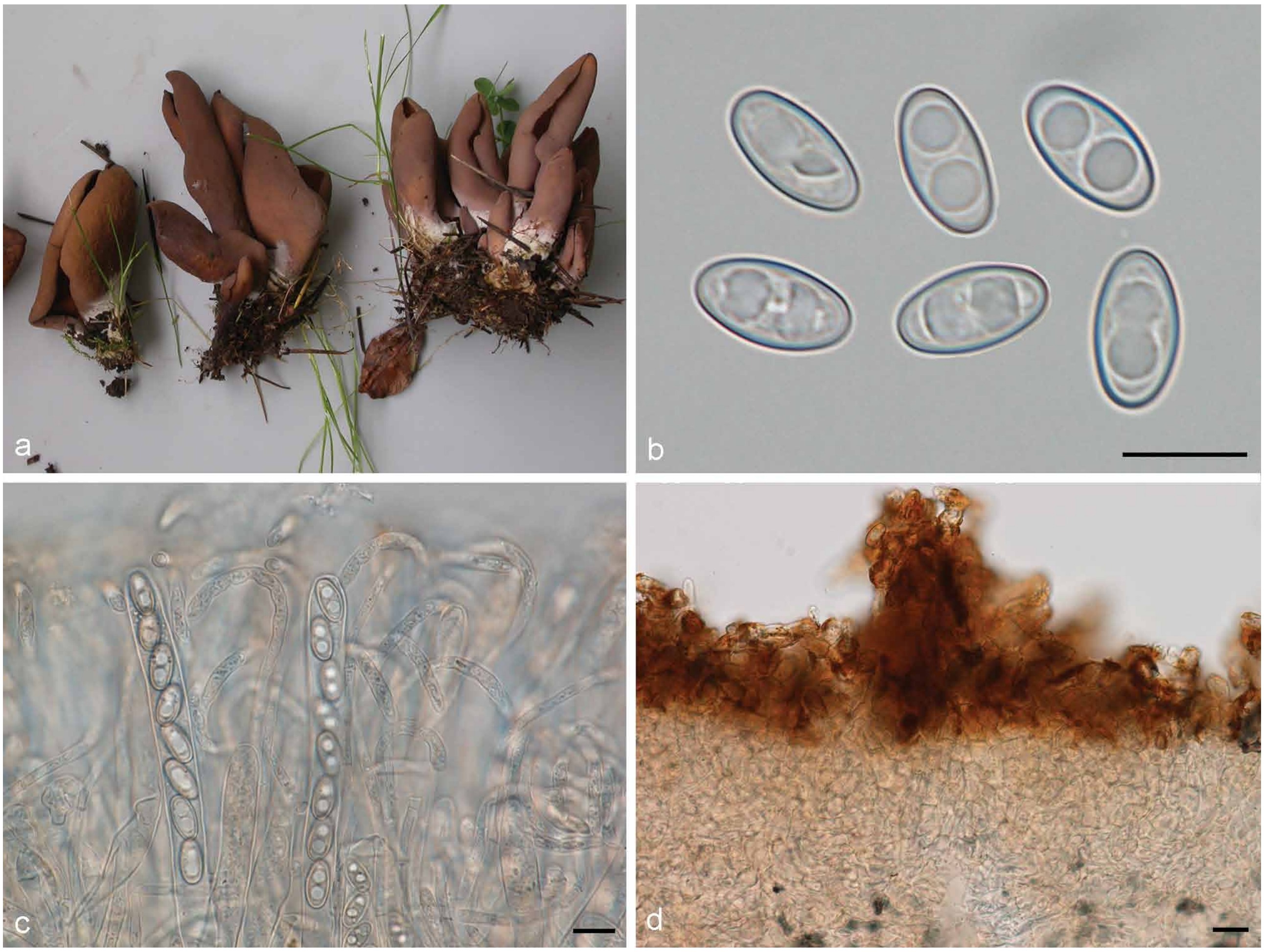

Fig. 27 *Otidea smithii* (ECV3345). a. Apothecia; b. spores in water†; c. paraphyses in water†; d. ectal excipulum in water†. — Scale bars = 10 µm; † = dried material. — Photos: a. E. Vellinga.

Fig. 28 *Otidea borealis* (S-F242694, holotype). a, b. Apothecia; c. close-up of apothecia showing a warty external receptacle and dentate margin; d. Young narrowly cup-shaped apothecium. — Photos: M. Carbone.

4–14(–21) µm wide, sometimes slightly swollen, thin-walled to slightly thick-walled, light brown, seldom with light brown resinous exudates at septa. *Ectal excipulum* of *textura angularis*, 70–100 µm thick, cells thin-walled to slightly thick-walled, pale brown, 13–30 × 8–15 µm. Surface with conical warts, 34–71 (–102) µm high, formed by short, fasciculate, hyphoid hairs, of 2–5 subglobose to elongated cells, constricted at septa, 6–14 µm wide, sometimes with a gelatinous sheath. Resinous exudates rather abundant on the outside, dark brown, partly dissolving and turning reddish in MLZ. *Basal mycelium* of 3–5 µm wide, light to darker brown hyphae, sometimes with pale brown drops on the surface, with abundant small, rod-shaped to irregular, brown resinous exudates.

Specimens examined. Canada, British Columbia, Goldstream Park, Victoria, on decayed wood under mature Douglas fir, 21 Sept. 1968, *J. Ginns* 1212 (UPS F-629486). – USA, California, Alameda Co., Berkeley, Le Conte Avenue, in lawn under *Betula* and *Cedrus*, 25 Oct. 2005, *E. Vellinga*, ECV3345 (S); California, Del Norte Co., California State Park, Lake Earl Wildlife Area, access by Sand Hill Road, with *Abies grandis*, *Picea sitchensis*, *Polystichum munitum*, *Rubus spectabilis*, *Vaccinum ovatum*, 15 Dec. 1997, *M. Madsen & R. Davis* (OSC 56823); Oregon, Benton Co., Philomath, Woods Creek Road, 15 Nov. 1997, *E.T. Peterson* (OSC 56811); Washington, Pierce Co., Mt Rainier National Park, Lower Tahoma Creek, 30 Oct. 1996, *E.T. Peterson* (OSC 56753); ibid., 18 Oct. 1997 (OSC 56799); Washington, Lewis Co., Gifford-Pinchot National Forest, Camp Creek Falls Trail, on litter with *Acer circinatum*, *A. macrophyllum*, *Tsuga heterophylla*, *Berberis nervosa*, *Polystichum munitum*, *Linnaea borealis*, *Rubus* sp., *Goodyera oblongifolia*, 6 Nov. 1997, *E. Hathaway & E. Millian* (OSC 56830).

Notes — *Otidea smithii* is closely related to *O. bufonia* and *O. mirabilis*, as shown by morphological and molecular characters. These three species share dark brown apothecia, brown basal tomentum and dark brown resinous exudates in the ectal excipulum. *Otidea smithii* is distinguished by shorter spores with a lower Q_m value, and typically narrower, ear-shaped apothecia. The unique, biflabellate or striate exudates in the medullary excipulum, as seen in *O. bufonia* and *O. mirabilis* (Fig. 4c, d), respectively, are not present in *O. smithii*. Only pigmented resinous exudates at the hyphal septa in the medullary excipulum are rarely found in *O. smithii* (as in Fig. 4a). *Otidea smithii* is so far only known from Western North America (Kanouse 1949, Peterson 1998). Our ITS sequence of *O. smithii* (JN942771) is identical to the ITS sequence of the holotype (AF072065).

Otidea concinna clade

Apothecia cup-shaped, split or sometimes entire, often with bright yellow tones. Spores small, 10–12.5 µm long, smooth. Paraphyses typically straight and claviform at apices. Basal mycelium with scattered reddish or yellow resinous exudates.

Species — *Otidea borealis*, *O. caeruleopruinosa*, *O. concinna*, *O. flavidobrunneola*, *O. lactea*, *O. minor*, *O. oregonensis*, *O. phlebophora*, *O. rainierensis*, *O. sinensis*, *O. tianshuiensis*, *O.* sp. 'a'.

25. *Otidea borealis* M. Carbone, Olariaga, K. Hansen & Van Vooren, *sp. nov.* — MycoBank MB809250; ITS barcode GenBank KM010023; Fig. 28, 30

Etymology. Referring to a supposedly boreal distribution.

Holotype. Finland, Koillismaa, Kuusamo, Juuma, Jäkälävuoma, western part of Jäkälävuoma gorges, many apothecia in moist soil among mosses at brookside, under *Picea abies*, 16 Aug. 2010, *M. Carbone* (S-F242694). *Isotype* (TUR-A 198578).

Apothecia gregarious to caespitose, 12–22 mm high, 8–15 mm wide, initially narrowly ear-shaped, upper margin subacute to rounded, then broadly ear-shaped, split, stipitate. *Hymenium* pale yellowish ochre (4A2, 5A2), when dried greyish ochre (4A2, 5A2). *Receptacle surface* ochraceous yellow (4A5, 5A5), yellowish brown (5B5, 5B6) in some parts, sometimes brown (5D7) in the margin, hygrophanous, when dried reddish brown (6D5, 6D6), warty, seldom slightly wrinkled at the base. Margin sometimes finely dentate and darker. Warts broadly conical, gregarious, light to dark brown. *Stipe* well developed, 3–12 × 2–6 mm. *Basal tomentum and mycelium* white to very pale yellow (3A2), when dried very pale yellow (3A2). *Spores* broadly ellipsoid, symmetrical, with two large guttules, smooth, hyaline, (10–)10.5–11.5 × 6–7 µm (L_m = 10.5 µm, W_m = 6.5 µm, Q_m = 1.7; n = 1). *Paraphyses* straight to curved, very few hooked, 2–2.5 µm wide, at apices up to 3–4.5(–5) µm wide, without notches, terminal segment 33–47 µm long, narrowly claviform to claviform, when dried containing slightly refractive, hyaline granules. *Asci* 167–198 × 9–10.5 µm. *Apothecial section* 1 000 µm thick. *Subhymenium* c. 100 µm thick, of dense *textura intricata*, cells 2–4 µm thick. *Medullary excipulum* 600 µm thick, of *textura intricata*, hyphae thin-walled to slightly thick-walled, 4–7 µm wide, hyaline, without resinous exudates. *Ectal excipulum* of *textura prismatica*, 80 µm thick, cells thin-walled, hyaline, unchanged to very pale yellow in KOH, 10–21 × 8.5–11 µm. Surface with broadly conical warts, 63–90 µm high, formed by fasciculate, short, hyphoid hairs, of 3–6 subglobose to ovoid cells, constricted at septa, 6–12 µm wide. Non-warted parts with single, 2–5-celled hyphoid hairs, with cylindrical to claviform upper cell, 45–73 × 8–10 µm. Resinous exudates golden brown, partly dissolving in MLZ (amber drops not observed), bright yellow and partly dissolving in KOH. *Basal mycelium* of 3–4.5 µm wide, very pale yellow hyphae, bright yellow in KOH, with spheroid to rod-shaped, reddish yellow resinous exudates, dissolving in MLZ, partially dissolving and turning bright yellow in KOH.

Other specimens examined. *Otidea* sp. 'a' — Sweden, Lappland, Arvidsjaurs, Lillån Allmänningreservat, 8 km SV Järvträsk, herb-rich *Picea* forest on calcareous ground, 12 Sept. 2009, *M. Karström*, MK0942 (S); ibid., 10 Sept. 2010, MK1081 (S).

Notes — Within the *O. concinna* clade, *O. borealis* is distinguished by broadly ear-shaped apothecia, with a pale yellowish ochre hymenium and a darker ochre yellow outer surface with small brown warts. Microscopically, the spores are proportionally broader than in closely related species, and the mycelium at the base of the apothecia turns bright yellow in KOH (tested in dried specimen only; Fig. 30f).

At least four species of the *O. concinna* clade have bright yellow outer apothecial colours, similar to *O. borealis*. *Otidea concinna* appears morphologically most similar, but besides the citrine-yellow outer receptacle, it differs in the narrower spores (Fig. 29) with higher Q_m value. *Otidea phlebophora* and *O. minor* are distinguished by the often entire apothecia with ribs or anastomosing veins at the base and distinctly narrower spores. *Otidea oregonensis* differs from *O. borealis* in typically having

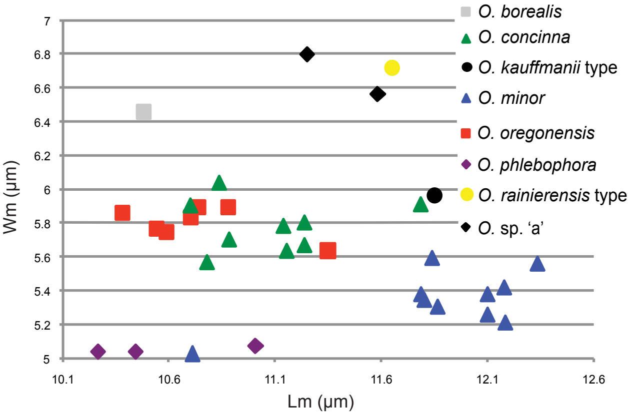

Fig. 29 Mean spore length and width in collections of species in the core of the *O. concinna* clade, based on 20 spores from each collection.

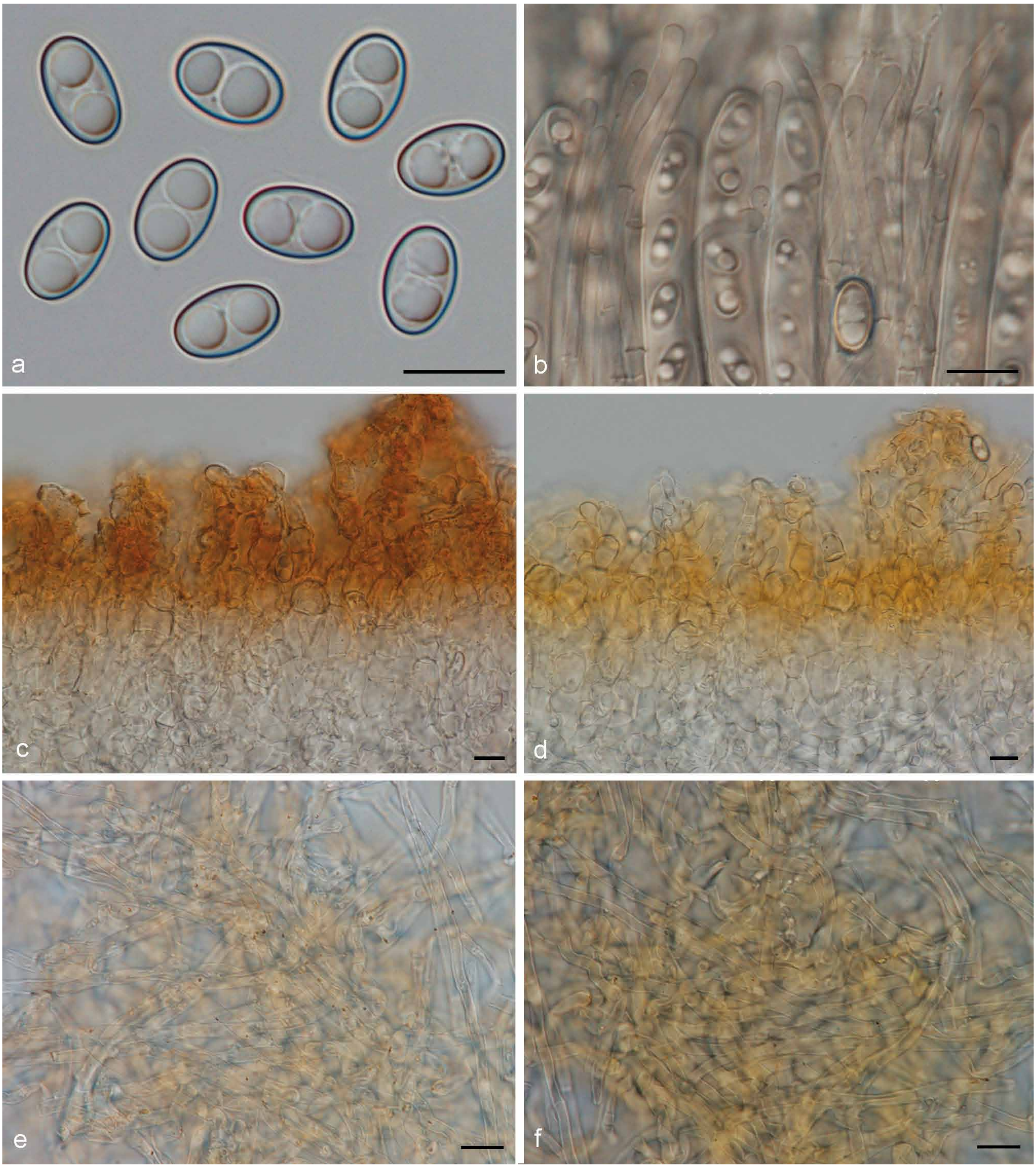

Fig. 30 *Otidea borealis* (S-F242694, holotype)†. a. Spores in water; b. paraphyses and asci in KOH; c. ectal excipulum in water, with resinous exudates on the outside; d. ectal excipulum turning bright yellow in KOH, resinous exudates partly dissolving; e. basal mycelium in water; f. basal mycelium in KOH. — Scale bars = 10 µm; † = all dried material.

obconical apothecia, sometimes with strongly rugulose base, citrine-yellow colour in the outer receptacle when young, narrower spores (Fig. 29), and the mycelium at the base of the apothecia does not turn yellow in KOH. The North American *O. rainierensis* (= *O. kauffmanii*) appears to have some yellowish apothecial pigment (see further under *O. rainierensis*). Nevertheless, the spores of *O. rainierensis* are longer than the spores of *O. borealis* (Fig. 29). Furthermore, our ITS-LSU phylogenies (Fig. 3) suggest that these species are distinct from *O. borealis*.

Two Swedish collections, MK0942 and MK1081, constitute another undescribed species (*Otidea* sp. 'a') nested within the *O. concinna* group. It resembles *O. borealis* in spore shape (only slightly longer in *Otidea* sp. 'a': 11–12(–13) × 6–7 µm; L_m = 11.2–11.6 µm, W_m = 6.6–6.8 µm, Q_m = 1.6–1.7; n = 2) and yellow reaction of the basal mycelium in KOH. The two *Otidea* sp. 'a' collections differ from *O. borealis* in the brownish ochre receptacle surface, without yellow tones, and ochre to pinkish ochre hymenium. Also our analyses of the ITS-LSU regions support *O.* sp. 'a' and *O. borealis* as distinct species (Fig. 3). Since only dried material has been available to us, we postpone a formal description of *O.* sp. 'a' until fresh and more abundant material, with good colour photographs, becomes available.

26. *Otidea caeruleopruinosa* Harmaja, Karstenia 48: 37. 2009 — Fig. 31

Holotype. FINLAND, Varsinais-Suomi, Lohja, Jalassaari, 20 Sept. 1978, *H. Harmaja* (H6010805) !

Apothecia gregarious to caespitose, 31–60 mm high, 17–50 mm wide, initially ear-shaped, upper margin rounded, then cup-shaped, split, margin sometimes lobulate, stipitate or sessile. *Hymenium* yellowish brown (5C6), when dried yellowish brown with a faint olivaceous tint (4D6) or orange-ochre (6B6, 6C6). *Receptacle surface* upper half concolorous with hymenium or slightly duller (5C5, 5C6), lower half more whitish (pubescent pruinose), slightly hygrophanous, when dried concolorous with hymenium towards the margin, below cream, or pale reddish brown (6C6), furfuraceous to very finely warty, seldom slightly ribbed at the base. Warts broadly conical, gregarious, paler or bluish. *Stipe* not well developed, rooting, up to 11 × 5 mm. *Basal tomentum and mycelium* abundant, when fresh ochraceous white, when dried light ochre (5A2). *Spores* narrowly ellipsoid to ellipsoid, often inequilateral, with two large guttules, smooth, hyaline, (10.5–)11–12.5 × 5.5–6.5 µm (L_m = 11.2–11.8 µm, W_m = 5.9–6.1 µm, Q_m = 1.9; n = 3). *Paraphyses* straight or curved, or broadly hooked, of the same width or broader at apices, 2–4(–5) µm wide, without notches, terminal segment 26–78 µm long, when fresh containing few, small, weakly refractive, pale guttules; when dried refractive, hyaline granules. *Asci* 144–200 × 9–11 µm. *Apothecial section* 700–950 µm thick. *Subhymenium* c. 70–80 µm thick, of 2.5–5 µm wide cylindrical cells, with scattered swollen, 12–18 µm wide cells, densely arranged. *Medullary excipulum* of *textura intricata*, 550–700 µm thick, hyphae thin to thick-walled, 3–9 µm wide, intercalated with swollen cells, 12–18 µm diam, hyaline, without resinous exudates. *Ectal excipulum* of *textura prismatica-angularis*, 100–120 µm, cells thin-walled, pale brown, sometimes yellow in KOH, 10–32 × 10–22 µm. Surface with conical to broadly conical warts, 60–80 µm high, formed by short, fasciculate hyphoid hairs, of 2–4 ovoid to cylindrical cells, 6–10 µm wide, not constricted at septa. Non-warted parts with single 2–7-celled hyphoid hairs, of globose to cylindrical cells, 20–33 × 9–17 µm. Resinous exudates abundant, yellow to reddish brown, dissolving in MLZ, bright yellow and partly dissolving in KOH and the outer excipulum turning bright yellow. *Basal mycelium* of 3.5–6(–8) µm wide hyphae, with spheroid to rod-shaped, reddish yellow resinous exudates, dissolving in MLZ, more slowly and partially dissolving in KOH, turning yellow.

Specimens examined. SPAIN, Girona, Ripollés, Setcases, under *Corylus avellana*, *Betula verrucosa* and *Buxus sempervirens*, on calcareous soil, 26 Aug. 2010, *M. Tabarés & S. Santamaría*, MT 10082601 (dupl. S). – SWEDEN, Södermanland, Nynäshamn, Herrhamra, on soil under *Fagus*, in narrow forest area along the road, 18 Sept. 2013, *I.-L. Walter*, KH.13.48 (S); Uppland, Älvkarleby, V from the train station, 24 Sept. 1950, *G. Fåhraeus & G. Stenlid* (UPS F-146664).

Notes — The main diagnostic characters of *O. caeruleopruinosa* are cup-shaped, split apothecia, whitish to pale cream hymenium, grey outside and rather small spores. Harmaja (2009a) described *O. caeruleopruinosa* with strong emphasis on the bluish shades of the warts on the apothecial outside, a character that has not been observed in our Swedish, or the Iberian material (Van Vooren et al. 2011). A third gathering from the Iberian site does not show bluish tones either (M. Tabarés, pers. comm.).

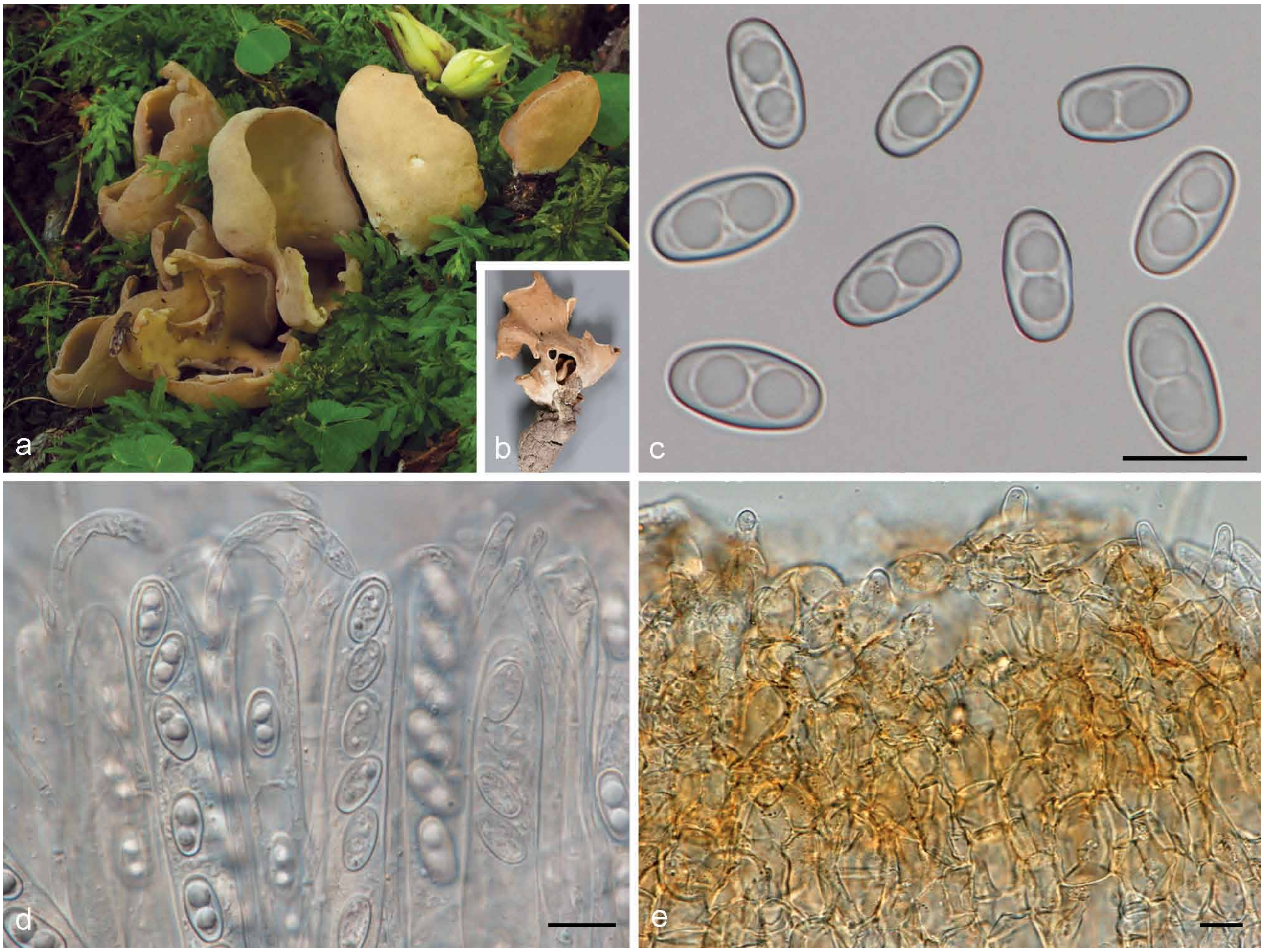

Fig. 31 *Otidea caeruleopruinosa*. a. Apothecia; b. apothecium showing basal tomentum†; c. spores in water†; d. paraphyses in water†; e. ectal excipulum in water† (a: MT 11080205; b–e: H6010805, holotype). — Scale bars = 10 µm; † = dried material. — Photos: a. M. Tabarés; b. J. Kearey.

Otidea caeruleopruinosa belongs to the *O. concinna* clade, and it shares several characters with the other members of the clade, such as cup-shaped apothecia, small spores, and an ectal excipulum of *textura prismatica* to *textura angularis*. It is morphologically most similar to *O. flavidobrunneola* (see Notes under that species).

27. ***Otidea concinna*** (Pers.) Sacc., Syll. Fung. 8: 96. 1889 — Fig. 32

Basionym. *Peziza concinna* Pers., Mycol. Eur. 1: 221. 1822: Fr., Syst. Mycol. 2: 49. 1822.

≡ *Helvella scutellata* Schaeff., Fung. Bavar. Palat. Nasc. 4: 101. 1774 ('*Elvela*').

Lectotype designated here: Schaeffer, Fung. Bavar. Palat. Nasc. 2: t. 150, f. 1. 1763 ('*Elvela tertia*'). *Epitype* designated here: Sweden, Uppland, Stockholm, Naturhistoriska riksmuseet, in front of the Botany building, under a big *Quercus robur* tree, by a row of *Populus*, 20 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.183 (S); MycoBank MBT178084.

= *Helvella pyxidata* Schaeff., Fung. Bavar. Palat. Nasc. 4: 111. 1774 ('*Elvela*').

≡ *Peziza marsupium* var. *pyxidata* (Schaeff.) Pers., Syn. Meth. Fung. 2: 640. 1801 ('ß *pyxidata*').

≡ *Scodellina pyxidata* (Schaeff.) Gray, Nat. Arr. Brit. Pl. 1: 669. 1821.

Misapplied names

– *Flavoscypha cantharella* sensu Harmaja, Karstenia 14: 107. 1974.

Apothecia gregarious to caespitose, 17–71 mm high, 12–66 mm wide, initially broadly ear-shaped, then soon expanding and becoming deeply cup-shaped, split, often broader above, very rarely entire when young, stipitate or broadly sessile. *Hymenium* pale yellowish ochre (3A3, 4A5) to pale greyish ochre (5A2),

Fig. 32 *Otidea concinna**. a, b. Apothecia; c. spores; d. paraphyses; e. ectal excipulum; f. basal mycelium (a, c, e, f: KH.09.183, epitype; b: KH.09.217; d: KH.09.176). — Scale bars = 10 μm; * = all fresh material.

sometimes with rose stains or spots, when dried light yellowish grey (2A2) to very pale yellowish ochre (3A2, 3A3). *Receptacle surface* bright citrine yellow (3A5–3A7), sometimes with a greenish hue (2A6), slightly hygrophanous, in drying slightly paler, fading to brownish ochre (4B5) in age, when dried yellow (3A7), furfuraceous, sometimes warty in young apothecia, sometimes shallowly wrinkled at the base. Warts flat to broadly conical, leaving a reticulum among them, concolorous. *Stipe* not well developed, rooting, 7–8 × 4–5 mm. *Smell* sweet, fruity, weak; taste mild. *Basal tomentum and mycelium* abundant, white to very pale cream (4A2), sometimes with very pale purplish tones, when dried white to very pale yellow (4A2). *Spores* narrowly ellipsoid to ellipsoid, inequilateral, with two large guttules, smooth, hyaline, (10–)10.5–12 × (5–)5.5–6.5 µm (L_m = 10.8–11.2 µm, W_m = 5.6–6 µm, Q_m = 1.8–2; n = 8). *Paraphyses* straight to bent, seldom broadly hooked, at apices claviform to abruptly capitate, 2.5–6(–8.5) µm wide, without notches, terminal segment 19–66 µm long, when fresh content hyaline homogenous or of small, refractive, hyaline to pale yellow granules; when dried refractive, hyaline granules. *Asci* 176–196 × 10–11.5 µm. *Apothecial section* 1200–2100 µm thick. *Subhymenium* c. 60–90 µm thick, composed of cylindrical cells, 2–4 µm wide, with scattered swollen cells, 9–13 µm wide, densely arranged. *Medullary excipulum* 600–1000(–1500) µm thick, of *textura intricata*, hyphae cylindrical to slightly swollen, 3–11(–15) µm wide, thin to thick-walled, hyaline, without resinous exudates. *Ectal excipulum* of *textura prismatica-angularis*, 80–100 µm thick, cells thin-walled, hyaline to very pale yellow, sometimes light reddish in KOH, 12–35 × 6–22 µm. Surface with low broadly conical warts, 60–70 µm high, formed by fasciculate, parallel, short, hyphoid hairs, of 4–6 ovoid cells, constricted at septa, 5–9.5 µm wide. Non-warted parts with single, 2–6-celled, hyphoid hairs, uppermost cell narrowly claviform to subcapitate, 20–45 × 4.5–7 µm, sometimes with a gelatinous sheath. Resinous exudates abundant, yellow or reddish, dissolving into amber drops in MLZ, turning bright yellow in KOH. *Basal mycelium* of cylindrical to slightly swollen, hyaline to very pale yellow hyphae, 3–4.5(–8.5) µm wide, yellow in KOH, with scattered, spheroid to rod-shaped, yellow or reddish resinous exudates, dissolving in MLZ, partially in KOH.

Specimens examined. Denmark, NE Sjælland, Jægersborg Dyrehave, 8 Sept. 1979, *H. Knudsen* (C-F-87186); NW Jylland, Nystrup Plantage, 'Kridtstien', on calcareous soil with *Abies*, 14 Sept. 1985, *T. Læssøe* (C-F-81617). – Estonia, Saaremaa, Abruka, ad terram, 16 Sept. 1966, *K. Kalamees* (UPS F-629562). – Finland, Varsinais-Suomi, Turku, Ispoinen Katariinanlaakso, W part of the reserve, in rich, essentially deciduous woods with *Corylus*, *Quercus*, *Tilia*, etc. on bare clayey mull soil, 22 Aug. 1977, *H. Harmaja* (S-F249360, ex-H6015773). – France, Saône-et-Loire, La Grande-Verrière, Senavelle, on the ground under *Pseudotsuga menziesii*, 12 Sept. 2008, *J.-P. Dechaume*, NV 2008.09.13 (dupl. S). – Spain, Huesca, Javierregay, humus of *Quercus rotundifolia* and *Q. humilis*, 5 Dec. 2009, *F. Prieto & A. González*, KH.09.250 (S); Huesca, Sallent de Gállego, Lanuza, 14 Oct. 2006, *I. Olariaga* (BIO-Fungi 13002); Huesca, Yebra de Basa, close to Sta Orosia chapel, in *Fagus sylvatica* forest, 11 Oct. 2009, *P. Siljeström* (ARAN-Fungi A8700091). – Sweden, Gotland, Ala, Stenstugu, near a big *Quercus robur* tree in meadow, on rich ground, among grass, 26 Sept. 2009, *E. Bohus-Jensen*, *K. Hansen & I. Olariaga*, KH.09.217 (S); Gotland, Lojsta, Lojsta slot, under *Corylus* on a chalk-rich slope, 19 Sept. 2000, *T. Knutsson*, TK2000-078 (S); Närke, Havsta, Bruntorpskärret, under conifers, 10 Aug. 2008, *B. Wasstorp*, JS.08.59 (S); Skåne, Degeberga, Segesholm, on a steep slope on bare ground, under *Fagus* and *Ulmus*, 23 Sept. 2010, *K. Hansen*, *K. Gillen*, *I. Olariaga*, KH.10.256 (S); Skåne, Fjälkstad, Balsberget, on rich ground among leaf litter under *Fagus*, 20 Sept. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.212 (S); Skåne, Kristianstad, N. Lingenäset, Storskogen, on ground in broadleaf forest, 18 Sept. 1996, *S.-Å. Hanson* s.n. (C); Uppland, Uppsala, Carolinaparken, under *Corylus avellana*, 7 Sept. 2010, *S. Ryman*, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.180 (S); Uppland, Uppsala, Hågadalen-Nåsten Nature Reserve, Predikstolen, under *Quercus robur*, *Ulmus glabra*, *Sorbus aucuparia*, with *Hepatica nobilis*, *Geum urbanum*, *Convallaria majalis*, on rich ground, 19 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.176 (S); ibid., 6 Oct. 2010, KH.10.182 (S).

Notes — *Otidea concinna* is characterised by cup-shaped, split apothecia, citrine yellow receptacle surface, along with paraphyses predominantly straight and claviform at apices. *Otidea minor* and *O. phlebophora* share with *O. concinna* a yellow receptacle surface, but they have anastomosing ribs at the apothecial base and narrower spores (Fig. 29). *Otidea oregonensis* is distinguished from *O. concinna* by the often obconical apothecia, sometimes with blunt ribs at the base.

The bright yellow receptacle surface is one of the main diagnostic characters of *O. concinna*, but we have observed the yellow colour can disappear with age, and the outer surface becomes brownish ochre (Fig. 32b) thus making it difficult to recognise the species. *Otidea rainierensis* is a North American taxon that shows an apothecial shape similar to *O. concinna*. Nevertheless, bright citrine yellow tones are absent in *O. rainierensis*, and our molecular data support it as distinct from *O. concinna* (Fig. 1, 3). For further comments see under *O. rainierensis*.

Nomenclatural notes — No authentic material has been located in Persoon's herbarium in L. We therefore select one element in Schaeffer's plate (t. 150, f. 1) as the lectotype, because it most closely resemble Persoon's description, showing two or more large, convolute, caespitose, sessile, cup-shaped apothecia with a citrine (although light) outer surface. Persoon (1822) collected the species in 'sylvula Vincennes prope Parisios' and Schaeffer's plate is from Bavaria, Germany. Fries sanctioned the name, but did not see material ('*v. ic.*', seen from icones). Nevertheless, we select a newly collected epitype from Sweden (Fig. 32a, c, e, f), associated with *Quercus* (the habitat described by Persoon) and backed by sequences of multiple gene regions (ITS, LSU, PRB1, RPB2 and EF1) of *O. concinna* collections from southern Europe (Spain) and from the epitype being identical (Hansen & Olariaga 2015), acknowledging the species is widely distributed in Europe.

28. ***Otidea flavidobrunneola*** Harmaja, Karstenia 48: 38. 2009 — Fig. 33

Holotype. Finland, Varsinais-Suomi, Lohja, Jalassaari, Ahtiala, Alho, Ahtiala Nature Reserve, rich, predominantly deciduous (*Quercus*, *Corylus* etc.) woods on calcareous soils, 20 Sept. 1978, *H. Harmaja* (H6010806) !

Apothecia gregarious to caespitose, 15–70 mm high, 8–50 mm wide, initially narrowly to broadly ear-shaped, then cup-shaped, split, margin sometimes lobulate, shortly stipitate or sessile. *Hymenium* cream or pale yellowish (4A2, 4A3), when dried orange-ochre (5B6). *Receptacle surface* pale brownish ochre (5A3, 5A4), slightly hygrophanous, when dried dark reddish brown (5E5), furfuraceous to very finely warty, seldom shallowly wrinkled at the base. Warts flattened, gregarious, concolorous. *Stipe* not well developed. *Basal tomentum and mycelium* abundant, white to pale cream (4A2) when fresh, ochre (5A4) to orange-ochre (6A4) when dried. *Spores* narrowly ellipsoid to ellipsoid, inequilateral, with two large guttules, very rarely with a third small guttule, smooth, hyaline, 9.5–11 × (4.5–)5–6 µm (L_m = 10–10.6 µm, W_m = 5.1–5.5 µm, Q_m = 1.9–2; n = 5). *Paraphyses* curved, a few straight or broadly hooked, of the same width or slightly broader at apices, 3–4 µm wide, without notches or slightly sinuous underside, uppermost cell 40–76 µm long, when fresh containing yellow guttules; when dried hyaline guttules or granules. *Asci* 127–170 × 9–10 µm. *Apothecial section* 900–1900 µm thick. *Subhymenium* c. 100 µm thick, of dense *textura intricata*, visible as a yellowish zone, cells cylindrical to slightly swollen. *Medullary excipulum* 600–1300 µm thick, of *textura intricata*, hyphae 5–13 µm wide, thick-walled, sometimes with a thinner outer wall, hyaline, without resinous exudates. *Ectal excipulum* of *textura prismatica*, sometimes of

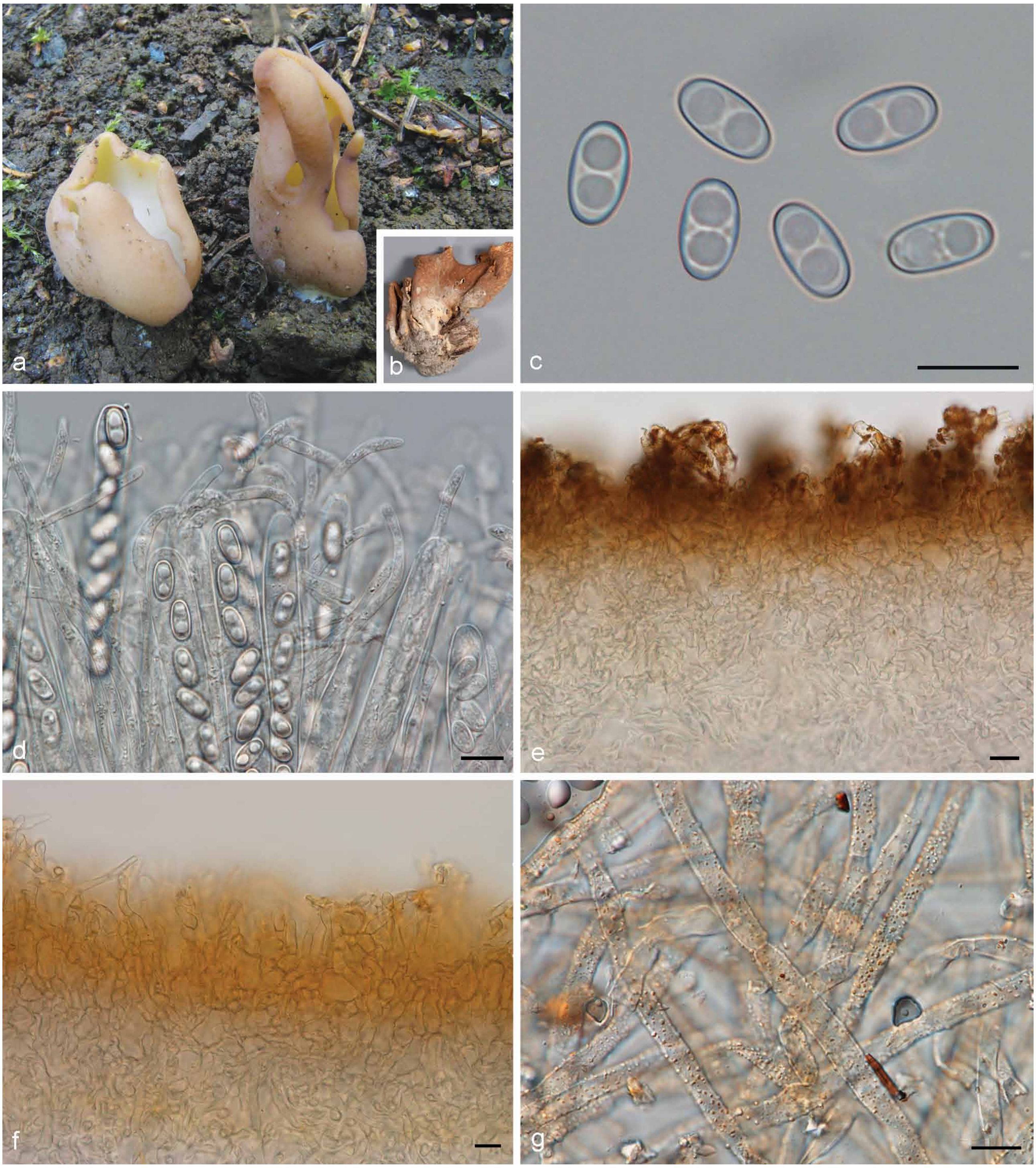

Fig. 33 *Otidea flavidobrunneola*. a. Apothecia; b. apothecium showing basal tomentum†; c. spores in water†; d. paraphyses in water†; e. ectal excipulum in water†; f. ectal excipulum in KOH†; g. basal mycelium in water† (a, c: KH.09.153; b, d–g: H6010806, holotype). — Scale bars = 10 µm; † = dried material. — Photos: b. J. Kearey.

a *textura angularis*, 100–120 µm, cells thin-walled, yellowish, distinctly citrine yellow in KOH, 18–38 × 11–13 µm. Surface with broadly conical warts, 40–70 µm high, formed by fasciculate, short hyphoid hairs, of 3–4 ovoid to elongated cells, constricted at septa, 5–9 µm wide, sometimes with a gelatinous sheath. Non-warted parts with 2–3-celled hyphoid hairs, with claviform uppermost cell, more rarely cylindrical, 33–55 × 8–13 µm. Resinous exudates abundant, yellowish brown, partially dissolving and turning slightly reddish in MLZ, partly dissolving, bright yellow and appearing gelatinous in KOH. *Basal mycelium* of 4–6 µm wide, hyaline to very pale yellow hyphae, with scattered swollen septa, with rounded to rod-shaped, yellow resinous exudates, slowly dissolving in KOH, quickly in MLZ.

Specimens examined. Finland, Uusimaa, Nurmijärvi, parish centre, under *Quercus*, 16 Sept. 1987, *P. Askola* 2220 (H); Uusimaa, Nurmijärvi, parish centre, clayey soil under *Quercus*, 11 Aug. 1988, *P. Askola* 2334 (H); Uusimaa, Nurmijärvi, parish centre, the margin of the park by the vicarage, under *Quercus*, 18 Aug. 1988, *P. Askola* 2360 (H). – Norway, Nord-Trøndelag, Leksvik, Gjøråsvika, on rich ground, on slope under *Corylus* and *Picea*, 3 Sept. 2009, *K. Hansen & I. Olariaga*, KH.09.153 (S). – Sweden, Uppland, Bondkyrka, Vårdsätra naturpark, 17 Aug. 1927, *H. Svensson* (UPS F-146554); Uppland, Uppsala, in front of the prison, on bare ground under deciduous trees, 14 Sept. 1938, *R. Gustafsson* (UPS F-146718).

Notes — *Otidea flavidobrunneola* is macroscopically characterised by cup-shaped, split apothecia, especially with age very pale yellowish brown outside and cream-white to pale yellow hymenium. Microscopically, the small spores and the yellow ectal excipulum turning brighter yellow in KOH are diagnostic. The apothecia and basal tomentum become characteristically darker upon drying: the outside turns dark brown, the hymenium and the basal tomentum orange ochre (Fig. 33b). *Otidea caeruleopruinosa* and *O. flavidobrunneola* are morphologically very similar, but differ in the spore sizes (L_m = 11.2–11.8 µm vs 10.1–10.6 µm) and colours of the basal tomentum in dried specimens. According to Harmaja (2009a), *O. flavidobrunneola* is reminiscent of *O. bufonia*, but the latter has a darker brown basal tomentum and larger, narrowly fusoid spores. We report here the first finds outside Finland.

29. *Otidea lactea* J.Z. Cao & L. Fan in Cao et al., Mycologia 82: 735. 1990

Holotype. China, Heilongjiang province, Yichun City, on ground (rotten wood?) under broadleaf trees, 6 Sept. 1987, *J.Z. Cao* (HMAS 61359, ex-MHSU 1803).

Notes — We were not able to get the material of *O. lactea* on loan, but it appears to be a distinct species based on the entire, cup-shaped, cream white apothecia and paraphyses with broadly clavate to subglobose apices (Cao et al. 1990). Also, in our LSU phylogeny (including a GenBank sequence of the holotype, DQ443447 from Liu & Zhuang (2006)), *O. lactea* forms a distinct sister lineage (ML 71 %, PP 99 %) to a clade of seven collections of *O. minor* from Europe (ML 95 %, PP 98 %, Fig. 1). *Otidea minor* differs from *O. lactea* in the (most often) split apothecia, with a yellow outer surface and often more narrow, straight to bent, subclaviform to claviform paraphyses apices. *Otidea lactea* has the characteristic broad apices of the paraphyses of the *O. concinna* clade, which however, in *O. lactea* becomes hooked with age (Cao et al. 1990). The holotype was originally deposited in MHSU (Cao et al. 1990), but later transferred to HMAS (confirmed by Hong-Mei Lu, HMAS).

30. *Otidea minor* (Boud.) Olariaga & K. Hansen, *comb. & stat. nov*. — MycoBank MB808975; Fig. 34

Basionym. *Otidea cantharella* var. *minor* Boud., Icon. Mycol. livr. 23: n°. 411. 1909 (preliminary text with 'circulaires').

≡ *Flavoscypha cantharella* var. *minor* (Boud.) Häffner, Rheinland Pfäl. Pilzj. 4: 36. 1994.

Lectotype designated here: Boud., Icon. Mycol. livr. 23: n°. 411, pl. 326. 1909; MycoBank MBT178086.

Misapplied names

– *Otidea cantharella* sensu Lundell & Nannfeldt, Fungi Exs. Suec. 1–2: 93. 1934.

– *Flavoscypha cantharella* sensu Dennis, Brit. Ascomyc.: pl. 8 D. 1978.

Apothecia gregarious to caespitose, 8–33 mm high, 4–41 mm wide, broadly ear-shaped or shallowly cup-shaped, often elongated on one side, normally split, often stipitate. *Hymenium* light ochre (3A2, 3A3) to yellowish grey (4A3), sometimes with weak rose stains or spots, when dried yellowish ochre (4A4, 4A5) to ochre (5A4). *Receptacle surface* citrine yellow (2A6, 2A7), slightly hygrophanous, in drying slightly paler, fading to brownish ochre (4B5, 4B6) in age, when dried reddish ochre (6B6–6D6) to reddish brown (5B4, 5B5), slightly furfuraceous to slightly warty, some apothecia with low ridges coming from the stipe, restricted to the base or reaching 1/2–1/3 of the apothecium, sometimes interconnected by low veins. Warts minute, conical, concolorous to brownish. *Stipe* often well developed, cylindrical, 2–12 × 2–5 mm. *Basal tomentum and mycelium* abundant, white, seldom with purplish tones, very pale yellow (4A2) when dried. *Spores* narrowly ellipsoid, often inequilateral, with two large guttules, smooth, hyaline, (10–)10.5–12.5(–13) × (4.5–)5–5.5(–6.2) µm (L_m = 10.7–12.3 µm, W_m = 5–5.6 µm, Q_m = 2.1–2.3; n = 10). *Paraphyses* straight to bent, seldom curved, subclaviform to claviform at apices, 3–8 µm wide, without notches, uppermost cell 20–71 µm long, when fresh with homogeneous content or seldom containing slightly refractive, light yellow granules at apices, often with a yellow refractive body (Fig. 34d); when dried small, slightly refractive, hyaline granules. *Asci* 153–169 × 9–10.5 µm. *Apothecial section* 750–1000 µm thick. *Subhymenium* c. 100 µm thick, of dense *textura intricata*, hyphae 3–6 µm wide. *Medullary excipulum* of *textura intricata*, 500–700 µm thick, hyphae 4–9(–13) µm wide, sometimes slightly swollen, thin to thick-walled, hyaline to very pale yellow, without resinous exudates. *Ectal excipulum* of *textura prismatica-angularis*, 80–150 µm, cells thin-walled, very pale yellow, unchanged in KOH, 10–33 × 6–15 µm. Surface with low flattened warts, 35–53 µm high, formed by short, fasciculate, hyphoid hairs, of 2–3 ovoid cells, constricted at septa, 6–9 µm wide. Non-warted parts with 2–4-celled hyphoid hairs, with subclaviform to claviform uppermost cell, 43–58 × 7.5–13 µm. Resinous exudates abundant, yellow or reddish to brownish yellow, dissolving into amber drops in MLZ. *Basal mycelium* of 3–7 µm wide, very pale yellow, slightly swollen hyphae, not changing in KOH, with very scattered amorphous or rod-shaped, yellow resinous exudates, dissolving in MLZ.

Specimens examined. Denmark, Jylland, Nystrup Plantage, Kridtstien, on calcareous soil under *Abies*, 1 Nov. 2007, *T. Læssøe*, TL-13332 (C); N Jylland, Rold Skov, Buderupholm Bjergskov, by fence of *Cypripedium*, calcareous soil along roadside, deciduous forest, 14 Sept. 1998, *K. Hansen*, KH.98.84 (C); Jylland, Vorsø, under *Salix caprea*, 25 Sept. 1981, *T. Læssøe*, TL-0684 (C); ibid., on base of *Salix caprea*, 8 Sept. 1982, *T. Læssøe*, TL-0754 (C); Sjælland, Geelskov, 10 km N of Copenhagen, 3 Aug. 1950, *M. Lange* (C-F-47967). – Finland, Helsinki, Toukola, Koreankatu, *Acer*, *Betula*, *Populus tremula*, *Salix caprea*, *Sambucus*, *Sorbus*, *Aegopodium podagraria*, *Urtica dioica*, 8 Sept. 1992, *R. Saarenoksa* 24592 (H); Varsinais-Suomi, Lohja, Pähkinäniemi, very rich, somewhat dry grass-herb forest with calcareous ground, 1 Aug. 1997, *U. Nummela-Salo & P. Salo* 4051 (H); Varsinais-Suomi, Lohja, Virkkala, NE-slope of Pähkinäniemi, very rich, somewhat dry grass-herb forest with calcareous soil, nearby *Corylus avellana*, *Populus tremula*, *Betula pendula*, 12 Sept. 2006, *U. Nummela-Salo & P. Salo* 10724 (H). – Italy, Calabria, Acri (CS), Croce di Greca, 14 Sept. 1995, *C. Lavorato*, CL 950914-01 (dupl. S). – Sweden, Gotland, Fårö, Avanäset, under *Pinus sylvestris*, on humus, sandy soil, 27 Sept. 2011, *J.C. Zamora*, KH.11.103 (S); Gotland, Lojsta hed, Russpark, grazed forest with *Pinus sylvestris*, on calcareous ground, 2 Oct. 2010, *K. Hansen*, *K. Gillen & I. Olariaga*, KH.10.311 (S); Småland, Stenbrohult, Stockanäs SSV of Stenbrohults kyrka, under *Pyrus*, *Salix* and *Prunus domestica*, 9 Aug. 2011, *G. Aronsson* (UPS F-548414); Södermanland, Södertalje, Mörkö, Oaxen, in rich soil in deciduous forest, *Corylus avellana*, *Salix caprea*, with *Lactarius citriolens*, 10 Sept. 1994, *P. Höljer* (H7003652); Uppland, Uppsala, the park in front of the prison, on bare soil, among needles etc. under *Abies*, 16 Aug. 1932, *S. Lundell* (S-F108335, Fungi Exs. Suec. 93); Öland, Högby, Horns kungsgårds Nature Reserve, under *Corylus*, 6 Aug. 2000, *T. Knutsson*, TK2000-057 (S).

Notes — *Otidea minor* is recognised macroscopically by apothecia with a yellow outside, and shallow ribs and veins at the base of at least some apothecia. *Otidea concinna* and *O. oregonensis* can be distinguished by the broader spores with a lower Q_m (Fig. 29). In fresh material of *O. minor*, some paraphyses had a strikingly, yellowish refractive body in the upper part, a so far unique feature within *Otidea*. To assess its taxonomic value, this feature has to be checked in additional fresh material and in closely related species.

Otidea minor has been confused with *O. phlebophora* due to the presence of ribs or veins at the base of the apothecia (Lundell & Nannfeldt 1934, Dennis 1978). Harmaja (2009a) proposed the provisional name *O. subconcinna* for *O. minor* as circumscribed here. After examining two collections annotated by him, we consider the Finnish material to be conspecific with our Swedish finds, based on both morphological and molecular data. Although Harmaja (2009a) did not directly compare *O. minor* (as *O. subconcinna*) and *O. phlebophora*, he stated in the key that *O. phlebophora* has 'other tinges of yellow' and mostly straight paraphyses. We could not confirm these differences in the material we examined. Instead, *O. minor* can be distinguished from *O. phlebophora* by the presence of at least some apothecia without ribs, and ribs when present shallower and less anastomosing, as well as normally split apothecia. In spite of their morphological similarity, *O. minor* and *O. phlebophora* are not sister species in our four-gene phylogeny, but both are deeply nested within the *O. concinna* clade (Hansen & Olariaga 2015; see also Fig. 3). Boudier´s plate under *Otidea cantharella* var. *minor* shows shallow ribs at the base of some apothecia, agreeing with our material, and as considered by Harmaja (2009a). No original material could be located in PC, and we therefore designate Boudier's plate as the lectotype.

31. *Otidea oregonensis* K. Hansen & Olariaga, *sp. nov.* — MycoBank MB808973; ITS barcode GenBank KM010048; Fig. 35

Etymology. Named after Oregon, the area where most of the specimens of this species have been collected.

Holotype. USA, Oregon, Douglas Co., Umpqua National Forest, Diamond Lake Ranger District, under *Pseudotsuga menziesii* and *Abies concolor*, 7 Nov. 2010, *J. Moore*, Moorefun 58 (OSC). *Isotype* (S).

Apothecia gregarious to caespitose, 12–48 mm high, 23–80 mm wide, shallowly to deeply cup-shaped, sometimes elongated on one side or obconical, split, seldom entire, sometimes stipitate. *Hymenium* greyish white (2A2) to pale ochre (4A2–4A4), sometimes with rose stains or spots, when dried pale ochre (4A2–4A4). *Receptacle surface* bright citrine yellow

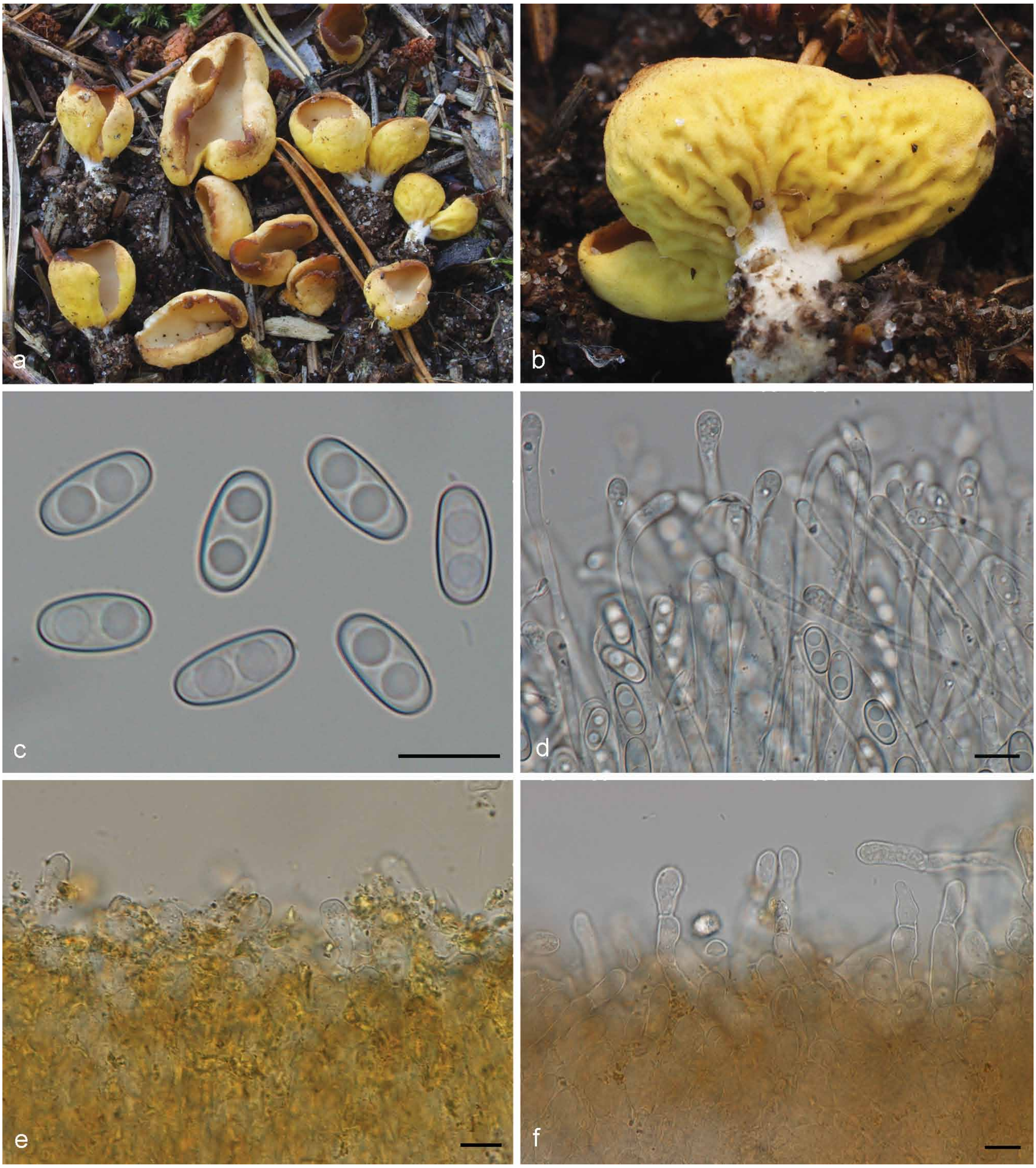

Fig. 34 *Otidea minor* (KH.10.311)*. a. Apothecia; b. apothecium showing veined outer receptacle; c. spores; d. paraphyses showing a crystallized body; e. ectal excipulum; f. ectal excipulum in Melzer's reagent, resinous exudates mostly washed away, showing free hypoid hairs. — Scale bars = 10 µm; * = fresh material.

(2A6–2A8), slightly hygrophanous, fading to brownish ochre (4B5, 4B6) in age, when dried brownish ochre (4A4, 4B4, 5B4), furfuraceous, sometimes some apothecia wrinkled-veined at the base, seldom with short ribs reaching up 1/3 to the margin, partly covered by white tomentum from the base. Warts sometimes present toward the base, minute, flat, concolorous. *Stipe* sometimes well developed, cylindrical, 3–18 × 3–11 mm. Smell mild. *Basal tomentum and mycelium* abundant, white, when dried very pale yellow (4A2). *Spores* narrowly ellipsoid to ellipsoid, sometimes inequilateral, with two large guttules, rarely with a few small granules, smooth, hyaline, 10–11.5 × 5.5–6(–6.5) µm (L_m = 10.4–11.3 µm, W_m = 5.6–5.9 µm, Q_m = 1.8–2; n = 7). *Paraphyses* bent to curved, sometimes straight, subclaviform to capitate at apices, 3–6(–8) µm wide, without notches, uppermost cell 28–70 µm long, when dried containing small, weakly refractive, hyaline granules. *Asci* 171–203 × 9–10.5 µm. *Apothecial section* 1000–1400(–2000) µm thick. *Subhymenium* 100–140 µm thick, of dense *textura intricata*, hyphae 2–4.5 µm wide, with scattered swollen, up to 12 µm wide cells. *Medullary excipulum* 650–850(–1400) µm thick, of *textura intricata*, hyphae 5–9(–17) µm wide, sometimes swollen, thin- to thick-walled, hyaline, without resinous exudates. *Ectal excipulum* of *textura prismatica* to *textura angularis*, 70–100 µm thick, cells thin-walled, very pale yellow, brighter yellow in KOH, 16–37 × 8–14 µm. Surface with low warts, 35–70 µm high, formed by short, fasciculate hyphoid hairs, of 2–4 ovoid cells, constricted at septa, 5–9 µm wide. Non-warted parts with 2–4-celled, hyphoid hairs, with claviform

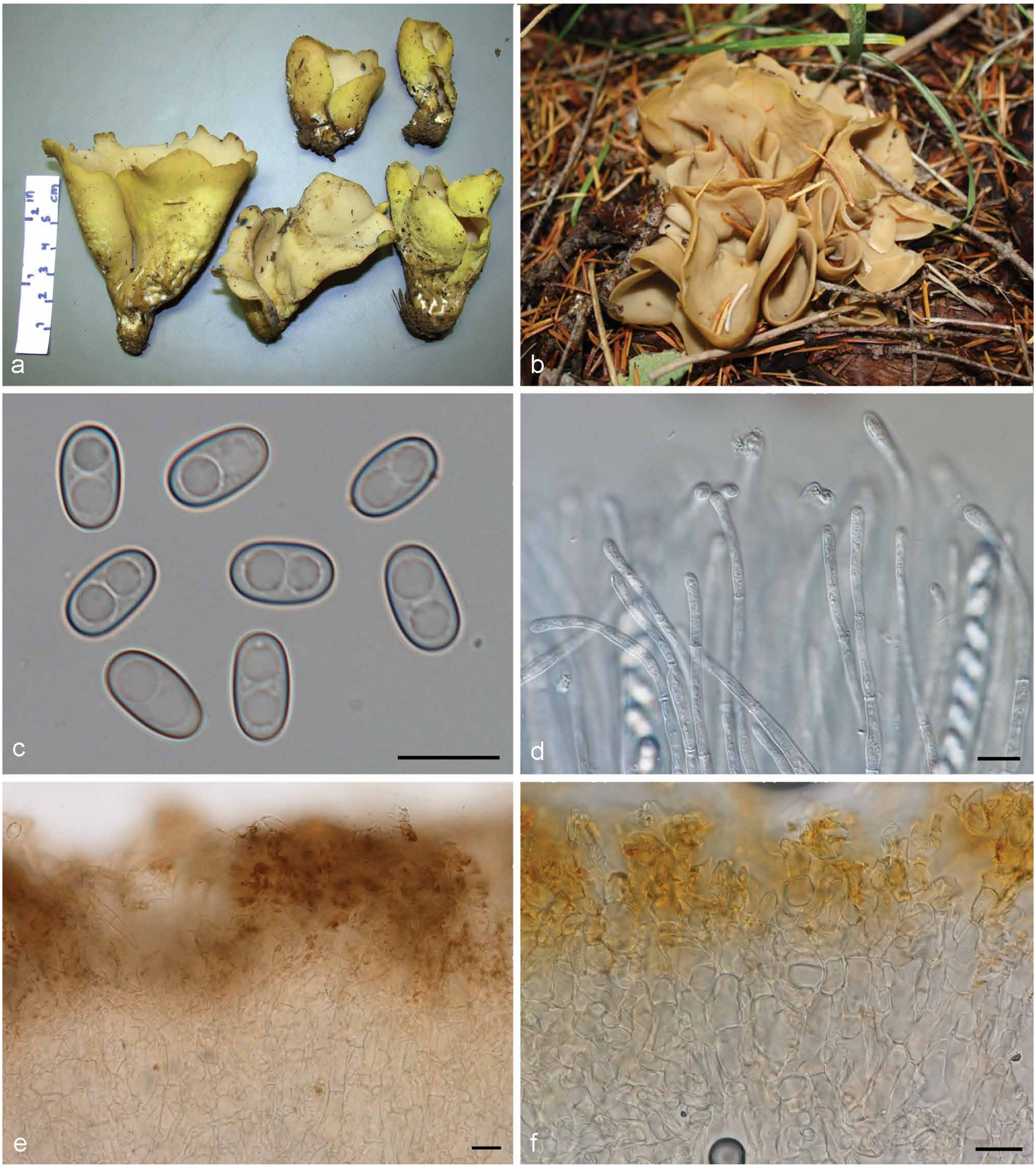

Fig. 35 *Otidea oregonensis*. a. Apothecia; b. apothecia showing faded colour in the outer receptacle; c. spores in water†; d. paraphyses in water†; e. ectal excipulum in water†; f. ectal excipulum in KOH† (a, c–f: Moorefun 58, holotype; b: rh139). — Scale bars = 10 µm; † = dried material. — Photos: a. J. Moore; b. R. Helliwell.

uppermost cell, 33–55 × 7–12 µm. Resinous exudates often abundant, yellow, dissolving into amber drops in MLZ, brighter yellow in KOH. *Basal mycelium* of 3–5(–8) µm wide, sometimes slightly swollen, very pale yellow hyphae, not changing in KOH, with very scattered, spheroid to rod-shaped, yellow resinous exudates, dissolving in MLZ.

Specimens examined. USA, Oregon, Jackson Co., Rogue River National Forest, under *Pseudotsuga menziesii*, *Abies concolor*, *Pinus ponderosa*, 2 Dec. 1999, *B. Schroeter* (OSC 72950); ibid., 27 Oct. 1990, *D. McKay*, NSW6354 (OSC 132740, dupl. S); Oregon, Josephine Co., Bureau of Land Management, Medford District, Grants Pass Resource Area, Little Pickett Creek, under *Pseudotsuga menziesii*, *Calocedrus decurrens*, *Lithocarpus densiflorus*, *Quercus chrysolepis*, 19 Dec. 2000, *R. Meyer* (OSC 108041); Oregon, Marion Co., near Breitenbush Hot Springs Community, 27 Oct. 1996, *J. Trappe* (OSC 56745); Oregon, Umpqua NF, Diamond Lake RD, under *Pseudotsuga menziesii*, 2 Nov. 2010, *J. Moore*, Moorefun 31 (S); ibid., old growth forest with *Abies concolor*, *Pseudotsuga menziesii*, 2 Nov. 2010, *R. Helliwell*, rh139 (OSC); Washington, Lewis Co., Gifford Pinchot National Forest, Camp Creeks Falls Trail, 6 Nov. 1997, *M. Castellano* (OSC 56829).

Notes — *Otidea oregonensis* is characterised by a citrine yellow receptacle surface, often a wrinkled to veined, or shallowly ribbed apothecial base, and relatively broad spores. The apothecia are typically obconical cup-shaped, with a narrow base. *Otidea oregonensis* was treated as *O. rainierensis* Kanouse by Peterson (1998), primarily based on the presence of swollen apices of the paraphyses. Also, one of the paratypes of *O. rainierensis* (EGS2179), sequenced by Peterson (1998), is nested within the *O. oregonensis* lineage in our ITS-LSU phylogeny (Fig. 3). Nevertheless, our sequences of the holotype of *O. rainieriensis*, from four different gene regions, show it belongs to another lineage, well separated from *O. oregonensis* (Hansen & Olariaga 2015). Kanouse´s concept of *O. rainierensis* was therefore mixed. The ITS-LSU phylogeny, including a larger sampling of the *O. concinna* clade, likewise resolves *O. oregonensis* as a distinct species.

Otidea phlebophora and *O. minor*, so far only known from Europe, resemble *O. oregonensis* in the cup-shaped apothecia with yellow outside and swollen paraphyses. *Otidea phlebophora* differs macroscopically from *O. oregonensis* in predominantly entire apothecia, with always a strongly veined-ribbed base reaching up 1/2 to the margin, while only small veins are present in some apothecia of *O. oregonensis*. Based on the material examined here, the slightly narrower spores in *O. phlebophora* (Q_m = 2–2.1 vs Q_m = 1.8–2 in *O. oregonensis*) are a constant and reliable character to separate these species (Fig. 29). *Otidea minor* tends to have smaller, shallower and more broadly cup-shaped apothecia than *O. oregonensis*. The spores of *O. minor* have a higher Q_m value (2.1–2.3) that does not overlap with the Q_m of *O. oregonensis*.

32. *Otidea phlebophora* (Berk. & Broome) Sacc., Syll. Fung. 8: 97. 1889 — Fig. 36

Basionym. *Peziza phlebophora* Berk. & Broome, Ann. Mag. Nat. Hist., ser. III, 18: 122. 1866.

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

Lectotype designated here: England, North Somerset, Brislington, 16 Sept. 1853 (K(M) 144045, ex Herb. C.E. Broome) !; MycoBank MBT178087.

Apothecia gregarious, 8–12 mm high, 3–40 mm wide, shallowly to deeply cup-shaped, sometimes elongated on one side, entire, seldom split, often stipitate. *Hymenium* pale ochre (4A2, 4A3), sometimes with rose stains or spots, when dried yellowish

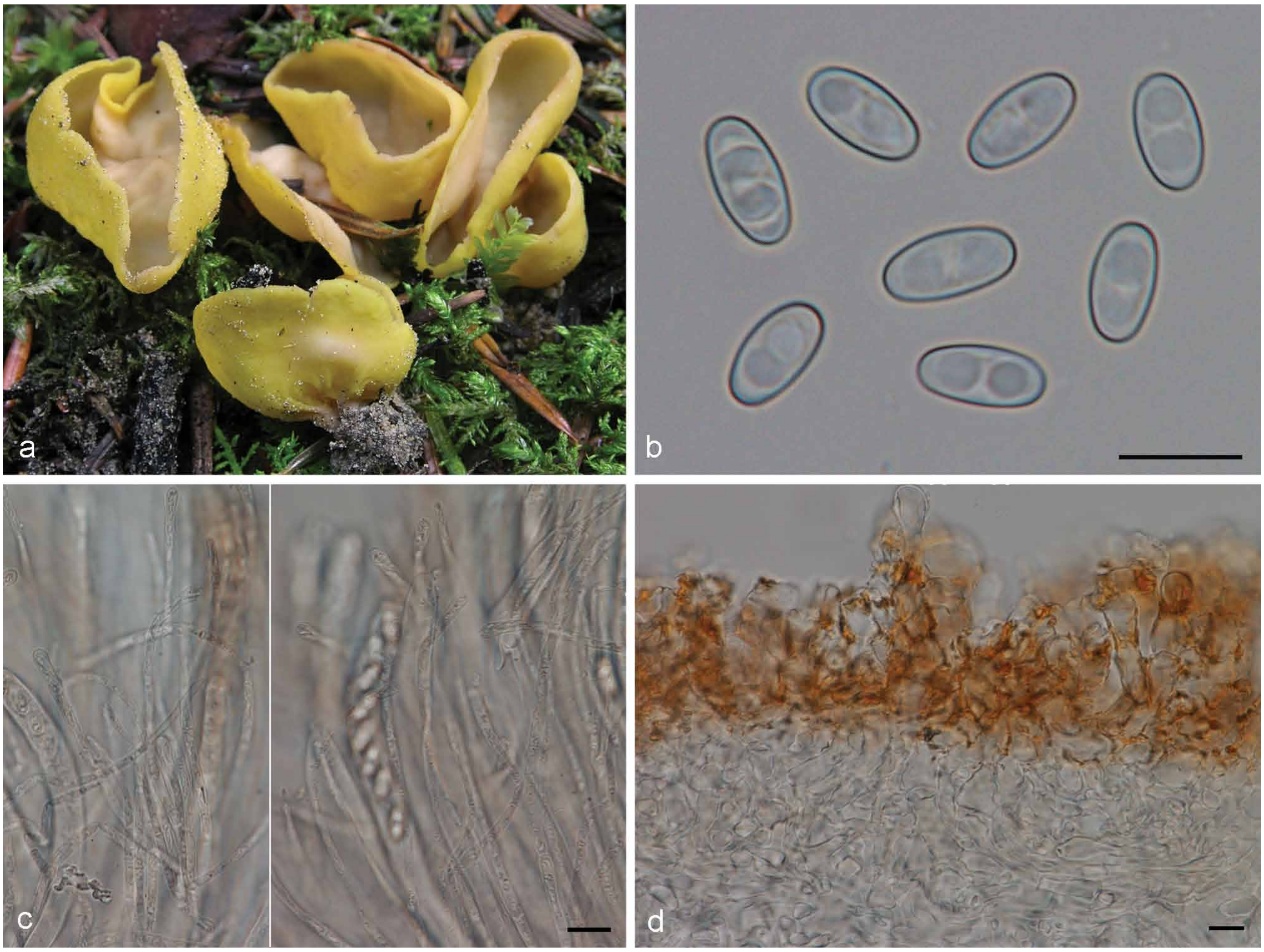

Fig. 36 *Otidea phlebophora* (JV06-385). a. Apothecia; b. spores in water†; c. paraphyses in water†; d. ectal excipulum in water†. — Scale bars = 10 µm; † = dried material. — Photos: a. J. Vesterholt.

ochre (4B4, 5B6, 5C6) to reddish brown (6C5, 6C6). *Receptacle surface* bright citrine yellow (3A7, 2A7), sometimes with a greenish hue (2A6), slightly hygrophanous, fading to brownish ochre (4B5) in age, when dried yellowish brown (5B6, 5C6) to reddish brown (6C6, 6D6), furfuraceous, with high ridges in the basal part of all apothecia reaching up 1/2–1/3 to the margin, interconnected by veins, partly covered by white basal tomentum. Warts minute, flat to rounded, appressed, concolorous. Stipe often well developed, cylindrical, 1–10 × 1.5–3 mm. *Basal tomentum and mycelium* abundant, white, very pale ochre (5A2) when dried. *Spores* narrowly ellipsoid, sometimes inequilateral, with two large guttules, smooth, hyaline, (9.5–)10–11.5(–12) × (4.5–)5–5.5(–6.2) µm (L_m = 10.2–11 µm, W_m = 4.9–5.1 µm, Q_m = 2–2.1; n = 5). *Paraphyses* straight to bent, cylindrical to claviform at apices, 2–3.5 µm wide, without notches, uppermost cell 23–46 µm long, when dried containing small, rather refractive, hyaline guttules. *Asci* 130–153 × 8–9 µm. *Apothecial section* 650–1000 µm thick. *Subhymenium* 80–100 µm thick, of dense *textura intricata*, hyphae 2–3 µm wide. *Medullary excipulum* of *textura intricata*, 450–650 µm thick, hyphae 4–7(–14) µm wide, sometimes swollen, thick-walled, hyaline to very pale yellow, without resinous exudates. *Ectal excipulum* of *textura prismatica-angularis*, 80–100 µm thick, cells thin-walled, hyaline to very pale yellow, unchanged in KOH, 15–21 × 6–11 µm. Surface with low flattened warts, 40–60 µm high, formed by short, fasciculate hyphoid hairs, of 3–4 ovoid cells, constricted at septa, 8–12 µm wide. Non-warted parts with 2–3-celled hyphoid hairs, with claviform uppermost cell, 30–60 × 7–13 µm. Resinous exudates abundant, yellow, dissolving into amber drops in MLZ. *Basal mycelium* of 3.5–7 µm wide, slightly swollen, very pale yellow hyphae, not changing in KOH, with very scattered, spheroid to rod-shaped, yellow resinous exudates, dissolving in MLZ.

Specimens examined. Denmark, NE Jylland, Rubjerg Knude Plantage, under *Abies* in large fairy ring, 28 Aug. 2006, *J. Vesterholt & L. Vesterholt*, JV06-385 (C); NE Sjælland, Ravnsholts Hegn, under *Picea abies*, 30 Aug. 1999, *B.W. Pedersen* (C-F-71506). – Finland, Varsinais-Suomi, Lohja, Jalassaari, Alho, by the Ahtiala manor, in rich forest with *Quercus robur*, *Corylus avellana*, *Prunus padus*, cultivated *Larix sibirica* and *Betula*, 30 Aug. 1967, *H. Harmaja* (H6010675). – Sweden, Dalarna, Husby, Husby värdhus, on lawn under *Quercus*, *Tilia*, *Larix* and *Acer*, 31 Aug. 1958, *R. Morander* (UPS F-144691); Skåne, Helsinborg, Jordbodalen by Harlyckan, on sandy ground in deciduous forest under *Quercus*, 13 July 1995, *S.-Å Hanson*, SÅH 30601 (C); Uppland, Djurö, Runmarö, Södersunda, in the city, on the ground under *Syringa*, 18 Sept. 1949, *G. Haglund & R. Rydberg* (S-F108338, UPS F-144689); Uppland, Uppsala, Sunnersta, Almlund, calcareous, humus-rich clay, 23 Aug. 1986, *J. Nitare* (UPS F-119845). – UK, Northamptshire, King´s Cliffe, on soil, 1853, *M.J. Berkeley* (K(M) 144046, syntype of *P. phlebophora*); North Somerset, Brislington, The Beeches, Sept. 1853, *C.E. Broome* (K(M) 194582, syntype of *P. phlebophora*).

Other specimen examined. *Otidea integra* — Italy, Sopramonte, 1892, *G. Bresadola* (S-F108342). Locality not specified, in silvis mixtis, 1892, *G. Bresadola* (PC 124965).

Notes — *Otidea phlebophora* is primarily characterised by high anastomosing ribs and veins towards the apothecial base. Diagnostic characters are in addition, the predominantly entire apothecia, with a citrine yellow outside. For a comparison with *O. concinna*, *O. minor* and *O. oregonensis* see Notes under those species. Harmaja (1986) elevated *O. integra* to species rank based on smaller apothecia and broader, curved paraphyses. The likely original specimen of *O. integra* collected in 1892 and kept in Bresadola's herbarium (S-F108342), shows curved paraphyses up to 5 µm broad, the same as Harmaja (1986, 2009a) gave for *O. phlebophora*. The paraphyses in the *O. phlebophora* material examined by us were straight to bent, and otherwise similar to the original material of *O. integra*. In spite of the morphological similarity, the ITS2 sequence of *O. integra* (281 bp obtained) is different from the ITS sequences of the material assigned to *O. phlebophora* by us, and we preliminary accept *O. integra* as a separate species. The position of *O. integra* is without support in our ITS-LSU phylogeny (Fig. 3).

Nomenclatural notes — Harmaja (1974: 107) indicated a lectotype of *O. phlebophora* at K, but he gave no collection number and the typification was not achieved. We have studied three of four syntypes at Kew and select here the richest collection containing ten apothecia as the lectotype. It conforms to the current interpretation of the name, with several entire apothecia (i.e. without a split), a ribbed-veined base seen on two of the apothecia (the others with the base glued to the cardboard), spores in the range 9.5–11.7 × 4.7–5.9 µm (L_m = 10.6 µm, W_m = 5.1 µm), paraphyses straight and enlarged at apices, and abundant yellow resinous exudates in the ectal excipulum that dissolve into amber drops in MLZ.

33. ***Otidea rainierensis*** Kanouse, Mycologia 41: 674. 1949

Holotype. USA, Washington, Pierce County, Lower Tahoma Creek, MT Rainier National Park, 23 Aug. 1948, *A.H. Smith 30553* (MICH 14410) !

= *Otidea kauffmanii* Kanouse, Mycologia 41, 6: 673. 1949.

Holotype. USA, Michigan, Lakeland, 18 July 1915, *C.H. Kauffman* (MICH 14409) !

Kanouse (1949) only had dried material of *O. rainierensis* and described the outside of the apothecia as 'ochraceous buff', 'cinnamon buff' to 'wood brown' and the hymenium as 'avellaneous', 'vinaceous buff' to 'drab grey'. For *O. kauffmanii* she had notes on fresh material and she separated it from *O. rainierensis* based on the presence of yellow tones in the apothecia (outside 'chamois' to 'ochraceous', hymenium 'cream buff'). We believe *O. rainierensis* does have yellow apothecial tones, as we observed small yellow resinous exudates (in water) in the type collection of *O. rainierensis*, and as observed in closely allied species the yellow colour can fade and almost disappear with age (Fig. 32b). Different spore sizes were also used to distinguish the two species. The spores of the holotype of *O. kauffmanii* are however, larger than noted in the protologue, 11.5–12.5 × 5.5–6.5 µm, L_m = 11.9 µm, W_m = 6 µm, Q_m = 2 (spores 8–10(–12) × 5–6(–7) µm in the protologue), and thus overlapping with the spores of the holotype of *O. rainierensis*, 11–12 × 6.5–7 µm, L_m = 11.7, W_m = 6.7 µm, Q_m = 1.7. We suggest *O. kauffmanii* and *O. rainierensis* constitute a single species, based on molecular and morphological study of the type material (Fig. 3). Our ITS sequences of the holotypes differ by 4 bp. See also comments on *O. microspora* under Excluded, dubious and imperfectly known taxa. *Otidea rainierensis* is characterised by a smooth apothecial base, long and relatively broad spores, compared to the rest of the species in the *O. concinna* clade, and by paraphyses with abruptly enlarged, broadly clavate to globose apices.

EXCLUDED, DUBIOUS AND IMPERFECTLY KNOWN TAXA

Cochlearia (Cooke) Lambotte, Mém. Soc. Roy. Sci. Liege, ser. 2. 14: 323. 1888

Nom. illegit. Art. 53.1, non *Cochlearia* L., Sp. Pl. 2: 647. 1753 (*Cruciferae*).

Basionym. *Peziza* subg. *Cochlearia* Cooke, Mycographia part 6: 252 ('Index Systematicus'). 1879.

Notes — Eckblad (1968) selected *Peziza cochleata* as the type species for the genus *Cochlearia* considering it a synonym of *Otidea*. However, Rifai (1968) had already selected *Peziza aurantia* as the type species, herewith making *Cochlearia* a synonym of *Aleuria*. He felt too much doubt had surrounded the identity of *P. cochleata* and it better not be selected as the type species.

Otidea abietina (Pers.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 330. 1870 ‘1869–1870’

Basionym. *Peziza abietina* Pers., Neues Mag. Bot. 1: 113. 1794: Fr., Syst. Mycol. 2: 47. 1822.
≡ *Discina abietina* (Pers.) Rehm, Rabenh. Krypt.-Fl., ed. 2, 3: 977. 1896.
≡ *Pseudotis abietina* (Pers.) Boud., Icon. Mycol. list prél. 600 sp.: 3 (unnumbered page). 1904.

Notes — Nannfeldt (1966) stated that the original material belongs to *Peziza badia*, but Harmaja (2009a) and Carbone (2010c) reported two collections in Persoon’s herbarium under *O. abietina* representing *O. propinquata* and a third collection *O. bufonia*. If typified with elements belonging to either *O. propinquata* or *O. bufonia*, the name *O. abietina* would take priority over any of those. *Otidea abietina* is the type species of the genus *Pseudotis* (Boud.) Boud. The identity of *Pseudotis* will thus remain open until *O. abietina* is clarified or typified. Another way to typify *O. abietina* would be to select an element belonging to *Peziza badia*. However, this choice should be studied more thoroughly, since it would make *Pseudotis* available as a genus name for the *Peziza depressa-Ruhlandiella* lineage, if *Peziza* is split into smaller genera in the future (Hansen et al. 2005). For the time being we regard *O. abietina* as a *nomen ambiguum*, as several others (Harmaja 2009a, Carbone 2010c, Parslow & Spooner 2013).

Otidea alba Velen., Monograph. Discom. Bohemiae 1: 354. 1934

Holotype. Czech Republic, Karlštejn, Sept. 1924, *Fechtner* (PRM 149788) !

Notes — The holotype specimen has the typical oblong spores of the *O. alutacea* complex, (13.5–)14.5–16.5(–17.5) × 6.5–7.5 µm (L_m = 14.9 µm, W_m = 6.9, Q_m = 2.1). Judging from the spore size, *O. alba* might represent either *O. alutacea* s.str. or the *O. alutacea* clade 3b. It should be considered in future studies of the complex.

Otidea aurantia (Pers.) Massee, Brit. Fungus-Fl. 4: 448. 1895

Basionym. *Peziza aurantia* Pers., Observ. Mycol. 2: 76. 1800: Fr., Syst. Mycol. 2: 49. 1822.

Notes — This is the type species of *Aleuria*, *A. aurantia* (Pers.: Fr.) Fuckel.

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

Basionym. *Peziza aurantia* var. *atromarginata* W. Phillips & Plowr., Gard. Chron. 17: 191. 1882.

Notes — The blood red disc with short, obtuse, dark brown, 3–4 septate hairs, giving the margin a dark appearance suggest this may be a species of *Melastiza*. The spores are tuberculate with thread-like appendages.

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

Basionym. *Peziza aurantia* var. *stipitata* W. Phillips, Man. Brit. Discom.: 57. 1887.

Notes — The small, bright scarlet apothecia with a ‘stem equalling the height of the cup, 4 mm’ and the ornamented spores suggest this is a species of *Aleuria* or *Sowerbyella*. It was described as a variety of *Aleuria aurantia* (as *Peziza aurantia* Oed.). Ramsbottom (1914) cited *O. aurantia* var. *stipitata* as a synonym of *Sowerbyella rhenana* (as *Aleuria rhenana* Fuckel), but the type material is presumably lost (Spooner & Yao 1995) and no modern interpretation can be provided.

Otidea auriculariiformis Henn., Hedwigia 36: 232. 1897

Holotype. Brazil, *A. Glaziou* no. 20181 (S-F9965, ex Herb. Sydow) !

Notes — This species belongs to the genus *Phillipsia*, *Sarcoscyphaceae*. The large spores, (30.5–)31.5–36.5(–37) × 12.5–14.0 µm (L_m = 33.2 µm, W_m = 13.1 µm, from 13 spores), are ellipsoid, inequilateral in profile view, smooth or with faint cyanophobic, parallel, longitudinal ridges. Asci seem thick-walled, with an internal eccentric thickened apical pad. The medullary excipulum is of interwoven hyphae, running mostly parallel with the outer surface and the ectal excipulum is a narrow band of *textura prismatica*, with the long axes of the cells parallel to the exterior. The tropical distribution and the substrate, suggested in the diagnosis to be wood, are typical for *Phillipsia*.

Otidea cinerascens Velen., Novit. Mycol.: 152 .1947

Holotype. Czech Republic, Moravia, Žarošice, Aug. 1940, *V. Vacek* (PRM 151779).

Notes — The grey-ochraceous apothecia and spores with parallel sides suggest *O. cinerascens* belongs to the *O. alutacea* complex. Type not studied by us, but annotated in 2009 by B. Spooner as *O. alutacea* (a photograph of the collection and annotation provided by Jan Holec, PRM).

Otidea cochleata (L.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 329. 1870. ‘1869–1870’

Basionym. *Peziza cochleata* L., Sp. Pl. 4: 183. 1753: Fr., Syst. Mycol., Index: 129. 1832.
≡ *Cochlearia cochleata* (L.) Lambotte, Fl. Mycol. Belgique 1: 323. 1880.

Notes — The interpretation of the original description is difficult, but *O. cochleata* has been treated as a taxon in the *O. alutacea* group (e.g. Lundell & Nannfeldt 1938, Dissing 2000, Mornand & Courtecuisse 2005, Zhuang 2006), probably following Bulliard (1791: plate 154 as *Peziza cochleata*). Part of the Bulliard plate (f. b) has now been selected as the lectotype for *O. alutacea* (Carbone 2010a). The name *O. cochleata* should be considered in future revisions of the *O. alutacea* complex. For a review of the nomenclatural history of *O. cochleata* see Carbone (2010a) and Parslow & Spooner (2013).

Otidea darjeelensis (Berk.) Sacc., Syll. Fung. 10: 4. 1892

Basionym. *Peziza darjeelensis* Berk., Hooker’s J. Bot. Kew Gard. Misc. 3: 202. 1851.

Notes — Rifai (1968) stated that the type specimen of *P. darjeelensis* at Kew has iodine positive asci and echinulate spores, and does not belong to *Otidea*. Two collections of *P. darjeelensis* are present in Kew that may represent original material: India, Sikkim, *J.D. Hooker* (K(M) 177412, ex Herb. Berkeley); and India, Sikkim (K(M) 177413, ex Herb. Cooke). No annotation label by Rifai was found (B. Aguirre-Hudson, pers. comm.), but he most likely studied the collection from Berkeley’s herbarium, because he listed J.D. Hooker as the collector. The collection K(M) 177413 might be a part of K(M) 177412, because Cooke (1876, f. 215) illustrated *P. darjeelensis* from specimens in Berkeley’s herbarium. Both collections should be studied and a lectotype selected.

Otidea dochmia (Berk. & M.A. Curtis) Sacc., Syll. Fung. 8: 95. 1889

Basionym. *Peziza dochmia* Berk. & M.A. Curtis, J. Linn. Soc. Bot. 10: 364. 1869.
≡ *Phillipsia dochmia* (Berk. & M.A. Curtis) Seaver, N. Amer. Cup-fungi, Operc.: 184. 1928.

≡ *Aurophora dochmia* (Berk. & M.A. Curtis) Rifai, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., sect. 2, 57: 52. 1968.

Notes — This is the type species of the genus *Aurophora*. Rifai (1968) distinguished *Aurophora* from *Phillipsia* by its fan-shaped apothecia and the presence of a gelatinous matrix in the medullary excipulum.

Otidea domingensis (Berk.) Sacc., Syll. Fung. 8: 97. 1889

Basionym. *Peziza domingensis* Berk., Ann. Mag. Nat. Hist., ser. II, 9: 201. 1852.

Notes — This is the type species of the genus *Phillipsia*, *P. domingensis* (Berk.) Berk. (see Hansen et al. 1999).

Otidea doratophora (Ellis & Everh.) Sacc., Syll. Fung. 8: 96. 1888

Basionym. *Peziza doratophora* Ellis & Everh., J. Mycol. 1: 90. 1885.

Notes — The small spores and asci, along with the pointed paraphyses, suggest this taxon does not belong to *Otidea*. Cash (1953) proposed *O. doratophora* is a synonym of *Ionomidotis irregularis* (Schwein.) E.J. Durand (as *Midotis irregularis*).

Otidea euplecta (Cooke) Sacc., Syll. Fung. 8: 97. 1889

Basionym. *Peziza euplecta* Cooke, Mycographia part 3: 125. 1876.

Holotype. USA, Alabama, *Peters* 4560 (K(M) 161851, ex Herb. Berkeley as *Peziza phlebophora* var.) !

Notes — The type is in a poor condition: one apothecium immature; the other infected. But the species likely belongs to *Sarcoscypha*, *Sarcoscyphaceae*. The asci are inamyloid, thick-walled and with an eccentrically placed, thickened operculum, spores are ellipsoid, slightly inequilateral, 19–21 × 10.5–11 µm, smooth, and paraphyses straight, filiform, branching above. The excipulum is composed of interwoven hyphae that give rise on the outside to shallow pustules.

Otidea felina (Pers.) Bres., Fungi Trident. ser. 2, fasc. 14: 103. 1900

Basionym. *Peziza felina* Pers., Mycol. Eur. 1: 223. 1822.

Holotype. FRANCE, prope Pariseos, sylvula Meudon (L0116774, Herb. Persoon).

Notes — Van Vooren & Carbone (2012) revised the holotype and demonstrated that it belongs to the *O. alutacea* group. Parslow & Spooner (2013) considered *O. felina* a synonym of *O. alutacea*. Further studies on the *O. alutacea* group should consider the name *O. felina*, which might be epitypified for an unequivocal interpretation.

Otidea fibrillosa Massee, Brit. Fungus-Fl. 4: 449. 1895

≡ *Pseudaleuria fibrillosa* (Massee) J. Moravec (‘*Pseudoaleuria*’), Acta Mus. Morav. Sci. Biol. 88: 51. 2003.

Notes — According to Moravec (2005) this is a species of *Pseudaleuria*, *P. fibrillosa*.

Otidea grandis (Pers.) Boud., Bull. Soc. Mycol. France 9: 10. 1893

Basionym. *Peziza grandis* Pers., Ann. Bot. Usteri 15: 27. 1795.
≡ *Peziza abietina* var. *grandis* (Pers.) Pers., Mycol. Eur. 1: 233. 1822.
≡ *Aleuria grandis* (Pers.) Gillet, Champ. France Discomyc.: 42. 1879.
≡ *Scodellina grandis* (Pers.) Seaver, N. Amer. Cup-fung., Operc.: 186. 1928.

Notes — The original sense of *O. grandis* corresponds most likely to a species of the *Peziza depressa-Ruhlandiella* lineage (Hansen et al. 2005) due to the lack of a split. No original material of *O. grandis* seems to be kept in Persoon´s herbarium (L). The name *O. grandis* has been used for *O. bufonia* (Boudier 1905; specimen PC0093644 is *O. bufonia*) or *O. unicisa* (Kanouse 1949, Liu & Zhuang 2006). We regard it here as a *nomen dubium* and *confusum* in agreement with Harmaja (2009a).

Otidea grandis var. ***scheremetjeffii*** Henn., Hedwigia 42, 3: (116). 1903

Notes — Hennings (1903) described this taxon based on specimens kept in formalin and the colours provided in the protologue are probably imprecise. The spore size can fit *O. bufonia* or *O. onotica*, but there is no type material extant in B or S, and a precise interpretation cannot be proposed here.

Otidea harperiana Rehm, Ann. Mycol. 2: 34. 1904

Holotype. USA, Ohio, Blue Mountains, on ground, 6 June 1903, *Harper* 333 (S-F9961, ex Herb. Rehm, ‘Herb. R.A. and A.M. Harper 333’) !

Notes — This species is closely related or conspecific with *Peziza phyllogena* Cooke. The asci are strongly amyloid in MLZ with a general bluing over the apex and the spores are ornamented with irregular, low, separate warts that are higher and more densely placed at the poles (forming ‘pole caps’). Our spore measurements from the holotype, 18–19.5 × 8–9 µm (L_m = 18.6 µm, W_m = 8.5 µm, from 15 spores) are larger than those given in the protologue, 15–17 × 5–7 µm.

Otidea hirneoloides (Berk.) Sacc., Syll. Fung. 8: 96. 1889

Basionym. *Peziza hirneoloides* Berk. in Berkeley & Curtis, J. Linn. Soc. Bot. 10: 365. 1869.
≡ *Phillipsia hirneoloides* (Berk.) Berk., J. Linn. Soc. Bot. 18: 388. 1881.

Notes — The wood-inhabiting, ear-shaped apothecia, and especially, the cymbiform spores suggest this name is to be referred to *Phillipsia*. Hansen et al. (1999) suggested *P. hirneoloides* belongs to the *Phillipsia domingensis* complex.

Otidea lechria (Berk. & Broome) Sacc., Syll. Fung. 8: 97. 1889

Basionym. *Peziza lechria* Berk. & Broome, J. Linn. Soc. Bot. 14: 103. 1875.

Holotype. SRI LANKA, on rotten wood, Nov. 1867, *G.H.K. Thwaites* (K(M)161847, ex Herb. Berkeley).

Notes — B. Spooner annotated the holotype in 2008, and noted it has amyloid asci and belongs to *Peziza*.

Otidea lilacina R. Heim & L. Remy, Bull. Soc. Mycol. France 48: 65. 1932

Notes — The ornamented, multi-guttulate spores and straight paraphyses suggest that this taxon does not belong to *Otidea*. No original material could be traced in PC (B. Buyck, pers. comm.).

Otidea lobata Rodway, Pap. & Proc. Roy. Soc. Tasmania: 116. 1925 ‘1924’

Notes — Rifai (1968) stated that the type specimen appears to represent the inoperculate genus *Discinella*.

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

Basionym. *Peziza luculenta* Cooke, Mycographia part 3: 121. 1876.

Notes — The entire, orange apothecia and straight paraphyses with orange granules suggest this name does not belong to *Otidea*. Nannfeldt (1966) noted that *O. luculenta* has 'other affinities' than *Otidea*, but did not provide a generic placement.

Otidea luteonitens (Berk. & Broome) Massee, Brit. Fungus-Fl. 4: 449. 1895

Basionym. *Peziza luteonitens* Berk. & Broome, Ann. Mag. Nat. Hist., ser. II, 7: 180. 1851.

Notes — This name is currently placed in *Aleuria* as *Aleuria luteonitens* (Berk. & Broome) Gillet.

Otidea micropus (Pers.) Sacc., Syll. Fung. 8: 98. 1889

Basionym. *Peziza micropus* Pers., Icon. Desc. Fung. 2: 30. 1800: Fr., Syst. Mycol. 2: 54. 1822.

Notes — This name is a synonym of *Peziza varia* (Hedw.: Fr.) Fr. sensu Hansen et al. (2002).

Otidea microspora (Kanouse) Harmaja, Karstenia 15: 32. 1976

Basionym. *Otidea alutacea* var. *microspora* Kanouse, Mycologia 41: 668. 1949.

Notes — Kanouse (1949) described this taxon as a variety of *O. alutacea*. She indicated two different collections as the type; *A.H. Smith* 9351 after the diagnosis and *A.H. Smith* 17699 in the material examined. We have studied *A.H. Smith* 9351 (MICH 14406, dupl. UPS F-629985 !) and it has far larger spores than stated in the protologue (13–15.5 × 7–8 μm vs 9–10 × 5.5–6.5 μm). The oblong spores, an ectal excipulum of *textura angularis*, and the absence of yellow pigment in KOH indicate it belongs to the *O. alutacea* complex. As for *A.H. Smith* 17699 (UPS F-629996 !), the spores match the original description. The apothecial shape is similar to that of *O. rainierensis*. A GenBank ITS sequence of a paratype of *O. microspora* (*A.H. Smith* 30502) differs only 1 bp from the ITS sequence of the holotype of *O. rainierensis* (Fig. 3), but we prefer not to select a lectotype until all the original material has been examined. We therefore treat the name as doubtful for the time being.

Otidea neglecta Massee, Grevillea 22: 66. 1894

Notes — This name was erected as a new name for *O. auricula* in the sense of Rehm (1883), Saccardo (1889) and Bresadola (1884, as *Peziza*). The species that these three authors treated under the epithet *auricula* is *Wynnella silvicola* (Beck) Nannf. in its current sense.

Otidea obtecta (Schwein.) Sacc., Syll. Fung. 8: 98. 1889

Basionym. *Peziza obtecta* Schwein., Trans. Amer. Philos. Soc. ser. 2, 4: 170. 1832 '1834'.

Notes — The original description gives stipitate, 1–1.5 cm wide, cinnamon-coloured apothecia with a split, growing among leaves. Seaver (1928) stated that the identity of *O. obtecta* is uncertain. No original material could be located in PH and the identification of this species cannot be inferred.

Otidea olivacea Bucholtz, Bull. Soc. Imp. Naturalists Moscou 2: 325. 1897

Notes — The curved, uniguttulate spores and the occurrence on a rotten trunk suggest that this taxon does not refer to a species of *Otidea*. The Bucholtz herbarium was bought by the FH, but no authentic material of *O. olivacea* could be located there.

Otidea onotica var. ***ochracea*** (Fr.) Sacc., Syll. Fung. 8: 95. 1889

Basionym. *Peziza onotica* var. *ochracea* Fr., Syst. Mycol. 2: 48. 1822: Fr. loc. cit. ('ß *ochracea*').
≡ *Peziza ochracea* (Fr.) P. Karst., Not. Sallsk. Fauna Fl. Fenn. Forh. 10: 110. 1869.
≡ *Otidea ochracea* (Fr.) Seaver, Bull. Lab. Nat. Hist. Iowa State Univ. 5: 45. 1904.

Notes — Fries (1822) stated that this variety is close to *O. onotica*. It was elevated to species rank by Karsten (1869), who later considered it a synonym of *O. onotica* (Karsten 1871). As no original material exists and the original description is meagre, we are not able to provide a good interpretation of this taxon.

Otidea pleurota (W. Phillips) Sacc., Syll. Fung. 8: 97. 1889

Basionym. *Peziza pleurota* W. Phillips in Cooke, Mycographia part 5: 208. 1878.
≡ *Iotidea pleurota* (W. Phillips) Clem., Gen. Fungi: 175. 1909.
Holotype. ENGLAND, 1877, *W. Phillips* (K(M)29973).

Notes — Eckblad (1968) observed strongly amyloid asci in the type and concluded it belongs to *Peziza*. B. Spooner annotated the type as '*Peziza badiofusca* ?'.

Otidea radiculata (Sowerby) Bres., Fungi Trident. ser. 2, fasc. 11–13: 72. 1898

Basionym. *Peziza radiculata* Sowerby, Col. Fig. Engl. Fung. 1: 46 (unnumbered page), t. 114. 1797: Fr., Syst. Mycol. 2: 81. 1822.

Notes — This name is placed in *Sowerbyella*, as *S. radiculata* (Sowerby) Nannf. Yao & Spooner (2006) examined the type at K and confirmed its placement.

Otidea reisneri Velen., České Houby 4–5: 872. 1922

Notes — Svrček (1976) studied the type material and concluded it is a synonym of *Sowerbyella radiculata* (Sowerby: Fr.) Nannf.

Otidea schulzeri Quél. in Schulzer, Hedwigia 24, 4: 150. 1885

Notes — The apothecia of *O. schulzeri* were described as elongated on one side, split, pale yellow-grey and pseudostipitate. However, the very thick flesh (3–4 mm), the straight paraphyses and the spore size (20–28 μm) suggest this taxon does not represent *Otidea*. Also Nannfeldt (1966) stated that *O. schulzeri* could hardly belong to *Otidea*.

Otidea silvicola Beck in Sacc., Syll. Fung. 8: 97. 1889

Notes — This is *Wynnella silvicola*. The name was created for *Peziza atrofusca* Beck, a later homonym for *P. atrofusca* Berk. & M.A. Curtis.

Otidea sparassis Quél., Rev. Mycol. (Toulouse) 54: 65. 1892

Notes — The uniguttulate spores do not suggest an *Otidea*. This taxon might refer to a sparassoid *Helvella* species.

Otidea subonotica Henn., Hedwigia 36: 232. 1897

Notes — The original description does not provide any discordant feature for *Otidea*, except it was reported from Brazil.

No type material of *O. subonotica* exists in Hennings herbarium in B (Carbone 2009) or in S, and its correct placement cannot be inferred with certainty here.

Otidea succosa (Berk.) Thüm., Mycoth. Univ. 15: no. 1411. 1879

Basionym. *Peziza succosa* Berk., Ann. Mag. Nat. Hist., ser. I, 6: 358. 1841.

Notes — This is currently considered to be a species of *Peziza* s.l. (Hansen et al. 2005).

Otidea tasmanica Rodway, Pap. & Proc. Roy. Soc. Tasmania: 116. 1925 '1924'

Notes — Rifai (1968) studied the type specimen of *O. tasmanica* in Kew and synonymised it with *Peziza praetervisa* Bres. (sensu Dennis, as Rifai depicted ornamented spores from the type specimen). Thus, *O. tasmanica* might be close to, or a synonym of, *Peziza subviolacea* Svrček.

Otidea violacea A.L. Sm. & Ramsb., Trans. Brit. Mycol. Soc. 5: 237. 1916

Holotype. ENGLAND, Warwickshire, *W.B. Grove* 1915 (K(M) 30407, ex Herb. W.B. Grove).

Notes — Parslow & Spooner (2013) examined the holotype and concluded it is a species of *Peziza* (cf. *azureoides* Donadini).

Acknowledgements This monograph became more comprehensive thanks to the great efforts of numerous mycologists who provided us with interesting material. All our colleagues who contributed collections, discussed issues or helped us in other ways are warmly thanked. Especially we thank Nancy S. Weber, Rosanne Healy, Mats Karström and Tapio Kekki for putting at our disposal valuable material accompanied by colour photographs. We also thank the curators and staff in the herbaria mentioned in the taxonomic part, H.J.M. Sipman (B), M. Herrera and I. Salcedo (BIO), H. Knudsen (C), P.G. Jamoni and D. Bolognini (GMFN), D.H. Pfister and G. Lewis-Gentry (FH), P. Salo and S. Stenroos (H), E.D. Liu (HKAS), Hong-Mei Lu (HMAS), B. Aguirre-Hudson, B. Dentinger and B. Spooner (K), R. Rabeler and P. Rogers (MICH), D. McLaughlin (MIN), A.B. Mujic and J. Spatafora (OSC), B. Buyck (PC), A. Freire-Fierro (PH), J. Holec (PRM), S. Huhtinen (TUR, TUR-A) and R. Berndt (ZH), for searching material and arranging loans. We appreciate Kerstin Gillen´s assistance during fieldwork in 2010. Juan Santos and Xiang-Hua Wang collected part of the material during their participation in the Swedish Pezizomycetes project. We are indebted to Xiang-Hua Wang for sequencing a few important *Otidea* collections, for discussions and help in editing the manuscript, and Seppo Huhtinen for instructive discussions on resinous exudates. We thank D.H. Hawksworth and L.A. Parra for nomenclatural advice. Donald H. Pfister and Trond Schumacher reviewed the manuscript and we are grateful for their valuable comments and corrections. Funding for this research was provided by a grant from the Swedish Taxonomy Initiative to K.H. (grant no. 143/07 1.4).

REFERENCES

Arpin N. 1969. Les caroténoïdes des Discomycètes: essai chimotaxinomique. Bulletin Mensuel de la Société Linnéenne de Lyon 38 (suppl.): 1–169.

Batsch AJGK. 1783. Elenchus Fungorum. Halle, Germany.

Bonorden HF. 1851. Handbuch der allgemeinen mykologie als anleitung zum studium derselben, nebst speciellen beiträgen zur vervolkommung dieses zweiges der naturkunde. Schweizerbart, Stuttgart, Germany.

Boudier JLÉ. 1885. Nouvelle classification naturelle des Discomycètes charnus connus généralement sous le nom de Pezizes. Bulletin de la Société Mycologique de France 1: 91–120.

Boudier JLÉ. 1905. Icones Mycologicae, livr. 6. Klincksieck, Paris, France.

Boudier JLÉ. 1906. Icones Mycologicae, livr. 7. Klincksieck, Paris, France.

Boudier JLÉ. 1907. Histoire et classification des Discomycètes d'Europe. Klincksieck, Paris, France.

Boudier JLÉ. 1908. Icones Mycologicae, livr. 21. Klincksieck, Paris, France.

Boudier JLÉ. 1909a. Icones Mycologicae, livr. 23. Klincksieck, Paris, France.

Boudier JLÉ. 1909b. Icones Mycologicae, livr. 24. Klincksieck, Paris, France.

Boudier JLÉ. 1910. Icones Mycologicae, livr. 29. Klincksieck, Paris, France.

Bresadola G. 1884. Fungi Tridentini novi, vel nondum delineati, descripti, et iconibus illustrati. Ser. 1, fasc. 4–5: 43–70, pl. 46–75. Monauni, Trento, Italy.

Bresadola G. 1898. Fungi Tridentini novi, vel nondum delineati, descripti, et iconibus illustrati. Ser. 2, fasc. 11–13: 47–81, pl. 151–195. Zippel, Trento, Italy

Bresadola G. 1900. Fungi Tridentini novi, vel nondum delineati, descripti, et iconibus illustrati. Ser. 2, fasc. 14: 83–118, pl. 196–217. Zippel, Trento, Italy.

Bresadola G. 1933. Iconographia mycologica. Vol. XXV. Trento, Italy.

Bulliard JBF. 1791. Herbier de la France. Tome 11. Paris, France.

Cao JZ, Fan L, Liu B. 1990. Some species of Otidea from China. Mycologia 82: 734–741.

Carbone M. 2009. Il genere Otidea I. Sull'identità di Peziza onotica. Rivista di Micologia 52: 11–28.

Carbone M. 2010a. Il genere Otidea III. Identità e tipifizione di Peziza alutacea. Bollettino dell'Associazione Micologica ed Ecologica Romana 80–81: 22–38.

Carbone M. 2010b. Il genere Otidea IV. Prima parte. Otidea caligata, l'attuale nome di Otidea abietina sensu Breitenbach & Kränzlin, con discussione sull'abbandono dell'epiteto abietina. Schweizerische Zeitschrift für Pilzkunde 88: 14–17.

Carbone M. 2010c. Il genere Otidea IV. Seconda parte. Otidea caligata, l'attuale nome di Otidea abietina sensu Breitenbach & Kränzlin, con discussione sull'abbandono dell'epiteto abietina. Schweizerische Zeitschrift für Pilzkunde 88: 64–66.

Carbone M, Campo E, Vauras J. 2010. Records on Otidea mirabilis and O. tuomikoskii from Finland. Karstenia 50: 25–34.

Carbone M, Van Vooren N. 2010 '2009'. Il genere Otidea – II. Otidea fuckelii, una nuova specie pubblicata per chiarire le differenti interpretazioni di O. leporina. Rivista di Micologia 52: 313–330.

Cash EK. 1953. A record of the fungi named by J.B. Ellis. Part. II. The division of mycology and disease survey, special publication 2: 167–345.

Clements FE, Shear CL. 1931. The genera of fungi. Wilson, New York, USA.

Cooke MC. 1876. Mycographia seu Icones Fungorum. Part. 3. Williams & Norgate, London, Great Britain.

Cooke MC. 1878. Mycographia seu Icones Fungorum. Part. 5. Williams & Norgate, London, Great Britain.

Dennis RWG. 1978. British Ascomycetes. 2nd edn. Cramer, Vaduz, Germany.

Dissing H. 2000. Pezizales Bessey. In: Hansen L, Knudsen H (eds), Nordic Macromycetes. Vol. 1. Ascomycetes: 55–127. Nordsvamp, Copenhagen, Denmark.

Eckblad F-E. 1968. The genera of operculate Discomycetes. A reevaluation of their taxonomy, phylogeny and nomenclature. Norwegian Journal of Botany 15: 1–191.

Farr ML, Leeusink JA, Stafleu FA. 1979. Index Nominum Genericorum (Plantarum). Regnum Vegetabile vols. 100–102. Bohn, Scheltema & Holkema, Utrecht.

Franchi P, Lami L, Marchetti M. 1999. Helvella leporina, nome corretto per Helvella silvicola. Rivista di Micologia 42: 63–72.

Fries EM. 1822. Systema mycologicum. II. Officina Berlingiana, Sweden.

Fuckel L. 1870 '1869–1870'. Symbolae mycologicae. Jahrbücher des Nassauischen Vereins für Naturkunde 23–24: 1–459.

Gal M le. 1947. Recherches sur les ornamentations sporales des Discomycètes operculés. Bibliotheca Mycologica 28: 73–297. Reprint 1970. Cramer, New York, USA.

Gonnermann W, Rabenhorst L. 1869. Mycologia Europaea. Abbildungen sämmtlicher Schwämme Europas. 3. Dresden, Germany.

Gray SF. 1821. A natural arrangement of British plants. Baldwin, Cradock & Joy, London, United Kingdom.

Greuter W, Brummitt RK, Farr E, et al. (eds). 1993. Names in current use for extant plant genera. Regnum Vegetabile vol. 129. Koeltz Scientific Books, Koenigstein.

Häffner J, Winterhoff W. 1989. Rezente Ascomycetenfunde VI. Otidea apophysata (Cooke & Phill.) Sacc. ein extrem seltener Öhrling. Beiträge zur Kenntnis der Pilze Mitteleuropas 5: 175–184.

Hansen K, Læssøe T, Pfister DH. 2002. Phylogenetic diversity in the core group of Peziza inferred from ITS sequences and morphology. Mycological Research 106: 879–902.

Hansen K, LoBuglio KF, Pfister DH. 2005. Evolutionary relationships of the cup-fungus genus Peziza and Pezizaceae inferred from multiple nuclear genes: RPB2, ß-tubulin, and LSU rDNA. Molecular Phylogenetics and Evolution 36: 1–23.

Hansen K, Olariaga I. 2015. Species limits and relationships within Otidea inferred from multiple gene phylogenies. Persoonia 35: 148–165.

Hansen K, Perry BA, Dranginis AW, et al. 2013. A phylogeny of the highly diverse cup-fungus family Pyronemataceae (Pezizomycetes, Ascomycota) clarifies relationships and evolution of selected life history traits. Molecular Phylogenetics and Evolution 67: 311–335.

Hansen K, Pfister DH. 2006. Systematics of the Pezizomycetes - the operculate discomycetes. Mycologia 98: 1029–1040.

Hansen K, Pfister DH, Hibbett DS. 1999. Phylogenetic relationships among species of Phillipsia inferred from molecular and morphological data. Mycologia 91: 299–314.

Harmaja H. 1974. Flavoscypha, a new genus of the Pezizales for Otidea cantharella and O. phlebophora. Karstenia 14: 105–108.

Harmaja H. 1976. New species and combinations in the genera Gyromitra, Helvella and Otidea. Karstenia 15: 29–32.

Harmaja H. 1986. Studies on Pezizales. Karstenia 26: 41–48.

Harmaja H. 2009a. Studies in Otidea (Pezizales). Karstenia 48: 33–48.

Harmaja H. 2009b. A note on Otidea (Pezizales, Fungi). Phytotaxa 2: 49–50.

Hennings P. 1903. Beiträge zur Pilzflora Südamerikas. II. Hedwigia 36: 190–246.

Huelsenbeck JP, Larget B, Alfaro ME. 2004. Bayesian phylogenetic model selection using reversible jump Markov chain Monte Carlo. Molecular Biology and Evolution 21: 1123–1133.

Huhtinen S. 1990 ‘1989’. A monograph of Hyaloscypha and allied genera. Karstenia 29: 45–252.

Jamoni PG. 2001. Validazione di nuovi taxa. Funghi e Ambiente 85–86: 56.

Jamoni PG. 2004. I funghi dell’ambiente alpino – XVIII. Funghi e Ambiente 94–95: 5–19.

Kanouse B. 1949. Studies in the genus Otidea. Mycologia 41: 660–677.

Karsten PA. 1869. Monographia Pezizarum fennicarum. Notiser ur Sallskapets pro Fauna et Flora Fennica Forhandlingar 10: 99–206.

Karsten PA. 1871. Mycologia Fennica. Pars prima. Discomycetes. Bidrag till Kannedom of Finlands Natur och Folk 19: 1–263.

Kasparek F. 2000. Über einige bemerkenswerte Schlauchpilze. Der Tintling 19: 7–15.

Kimbrough JW. 1966. Studies in the Pseudoascoboleae. Canadian Journal of Botany 44: 685–704.

Kirk PM, Stalpers JA, Braun U, et al. 2013. A without-prejudice list of generic names of fungi for protection under the International Code of Nomenclature for algae, fungi, and plants. IMA Fungus 4: 381–443.

Korf RP. 1963. Discomycete flora of Asia, precursor II: A revision of the genera Acervus and Ascosparassis and their new positions in the Pezizales. Lloydia 26: 21–26.

Korf RP. 1972. Synoptic key to the genera of the Pezizales. Mycologia 64: 937–994.

Korf RP. 1973a. Sparassoid ascocarps in the Pezizales and Tuberales. Reports of the Tottori Mycological Institute 10: 389–403.

Korf RP. 1973b. Discomycetes and Tuberales. In: Ainsworth GC, Sparrow FK, Sussman S (eds), The fungi: An advanced treatise. Vol. 4A: 249–319. Academic Press, New York, USA.

Korf RP, Zhuang WY. 1991. A preliminary discomycete flora of Macaronesia: part 15, Terfeziaceae, and Otideaceae, Otideoideae. Mycotaxon 40: 413–433.

Kornerup A, Wanscher JH. 1961. Farver i farver. Politikens forlag, København, 1st edn.

Kumar S, Skjæveland Å, Orr RJS, et al. 2009. AIR: A batch-oriented web program package for construction of supermatrices ready for phylogenomic analyses. BMC Bioinformatics 10: 357.

Liu B, Cao JZ. 1987. Otideopsis yunnanensis gen. et sp. nov. of Pezizales from China and its position in Pezizales system. Journal of Shanxi University, Natural Science edition 4: 70–73.

Liu CY, Zhuang WY. 2006. Relationships among some members of the genus Otidea (Pezizales, Pyronemataceae). Fungal Diversity 23: 181–192.

Lundell S, Nannfeldt JA. 1934. Fungi Exsiccati Suecici, praesertim upsalienses Fasc. 1–2. Almqvist & Wiksells Boktryckeri, Sweden.

Lundell S, Nannfeldt JA. 1938. Fungi Exsiccati Suecici, praesertim upsalienses. Fasc. 11–12. Almqvist & Wiksells Boktryckeri, Sweden.

Lundell S, Nannfeldt JA, Holm L. 1985. Fungi Exsiccati Suecici, prasertim upsalienses. Fasc. 66 (No 3251–3300). Publications from the Herbarium, University of Uppsala, Sweden 18: 1–18.

Maas Geesteranus RA. 1967. De fungi van Nederland 2a. Pezizales – deel 1, Discinaceae, Helvellaceae, Morchellaceae, Pezizaceae, Rhizinaceae. Wetenschappelijke mededelingen van de Koninklijke Nederlandse Natuurhistorische Vereniging 69: 1–72.

McNeill J, Barrie FR, Buck WR, et al. (eds). 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. [Regnum Vegetabile No. 154.] Koeltz Scientific Books, Königstein, Germany.

Medardi G. 1995. Considerazioni sul genere Otidea Fuck., 1870. Bolletino del Circolo Micologico ‘G. Carini’ 29–30: 23–32.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov.: 1–8. New Orleans, LA, USA.

Moravec J. 1986. A new species and two new combinations in the genus Sowerbyella. Mycologia Helvetica 2: 93–102.

Moravec J. 1988. Sowerbyella angustispora spec. nov. and Otideopsis kaushalii comb. nov. (Discomycetes, Pezizales, Pyronemataceae). Mycologia Helvetica 3: 135–142.

Moravec J. 2005. A world monograph of the genus Cheilymenia (Discomycetes, Pezizales, Pyronemataceae). Libri Botanici 21: 3–256.

Mornand J, Courtecuisse R. 2005. Le genre Otidea et espèces affines en France. Bulletin mensuel de la Société linnéenne de Lyon 74, numero spécial: 65–84.

Nannfeldt JA. 1937. Contributions to the mycoflora of Sweden. 4. On some species of Helvella, together with a discussion of the natural affinities within the Helvellaceae and Pezizaceae trib. Acetabuleae. Svensk Botanisk Tidskrift 31: 47–66.

Nannfeldt JA. 1938. Contributions to the mycoflora of Sweden. 5. On Peziza catinus Holmskj. ex Fr. and P. radiculata Sow. ex Fr. with a discussion of the genera Pustularia Fuckel emend. Boud. and Sowerbyella Nannf. n. gen. Svensk Botanisk Tidskrift 32: 108–120.

Nannfeldt JA. 1966. On Otidea caligata, O. indivisa and O. platyspora (Discomycetes, Operculatae). Annales Botanici Fennici 3: 309–318.

Nei M. 1987. Molecular evolutionary genetics. Columbia University Press, USA.

Parslow M, Spooner B. 2013. The British species of Otidea: overview and the large spored species. Mycosystema 32: 347–365.

Pérez-Butrón JL, Fernández-Vicente J. 2008. Otidea apophysata, en la Península Ibérica. Errotari 5: 36–43.

Perry BA, Hansen K, Pfister DH. 2007. A phylogenetic overview of the family Pyronemataceae (Ascomycota, Pezizales). Mycological Research 111: 549–571.

Persoon CH. 1799. Observationes Mycologicae. Pars secunda. Leipzig & Luzern.

Persoon CH. 1822. Mycologia europaea. I. Erlangae, Germany.

Peterson ET. 1998. Systematics of the genus Otidea in the Pacific Northwest. Unpublished thesis. Oregon State University.

Pfister DH. 1979. A monograph of the genus Wynnea (Pezizales, Sarcoscyphacea). Mycologia 71: 144–159.

Pfister DH, Halling RE. 1989. Ascosparassis heinricheri from Venezuela: an extended distribution. Mycotaxon 35: 283–285.

Quélet L. 1886. Enchiridion fungorum in Europa media et praesertim in Gallia vigentium. Douin, Paris, France.

Rahm E. 1958. Otidea pusilla nov. spec. Zwerg-Öhrling. Schweizerische Zeitschrift für Pilzkunde 36: 33–35.

Rambaut A. 2002. Se-Al. Sequence Alignment Editor. Version 2.0 alpha 11. University of Oxford, Oxford. From http://tree.bio.ed.ac.uk/software/seal/.

Ramsbottom J. 1914. A list of the British species of Discomycetes arranged according to Boudier’s system, with a key to the genera. Transactions of the British Mycological Society 4: 343–381.

Rehm H. 1883. Ascomyceten XIV. Hedwigia 22: 1–18 (reprint).

Rifai MA. 1968. The Australasian Pezizales in the herbarium of the Royal Botanic Gardens Kew. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde, Tweede Reeks 57: 1–295.

Ronquist F, Teslenko M, Mark P van der, et al. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542.

Saccardo PA. 1884. Conspectus generum discomycetum hucusque cognitorum. Botanisches Centralblatt 18: 213–256.

Saccardo PA. 1889. Sylloge Fungorum omnium hucusque cognitorum 8. Patavii.

Schaeffer JC. 1763. Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur icons natives coloribus expressae. Tomus II. Regensburg, Germany.

Schaeffer JC. 1774. Fungorum qui in Bavaria et Palatinatu circa Ratisbonam nascuntur icons natives coloribus expressae. Tomus IV. Regensburg, Germany.

Seaver FJ. 1904. The discomycetes of eastern Iowa. Bulletin from the laboratories of natural history of the State University of Iowa 5: 230–297.

Seaver FJ. 1927. A tentative scheme for the treatment of the genera of the Pezizaceae. Mycologia 19: 86–89.

Seaver FJ. 1928. The North American cup-fungi (operculates). Reprint 1961. Hafner Publishing Company, New York, USA.

Smith ME, Healy RA. 2009. Otidea subterranea sp. nov.: Otidea goes below ground. Mycological Research 113: 858–866.

Sowerby J. 1797. Coloured figures of English fungi or mushrooms. Vol. I. London, England.

Spooner BM, Yao Y-J. 1995. Notes on British taxa referred to Aleuria. Mycological Research 99: 1515–1518.

Stamatakis A. 2006. Raxml-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690.

Svrček M. 1976. A taxonomic revision of Velenoský's types of operculate discomycetes (Pezizales) preserved in national museum, Prague. Sborník národního muzea v Praze. Acta Musei Nationalis Pragae 32 B: 115–194.

Taylor JW, Jacobson DJ, Kroken S, et al. 2000. Phylogenetic species recognition and species concepts in fungi. Fungal Genetics and Biology 31: 21–32.

Thiers B (ed). 2014. Index Herbariorum. A global directory of public herbaria and associated staff. New York Botanical Garden´s Virtual Herbarium. http://sweetgum.nybg.org/ih/.

Van Vooren N. 2010. Note sur Otidea mirabilis (Pezizales). Ascomycete.org 2: 33–35.

Van Vooren N. 2011a. Le genre Otidea V. Otidea apophysata et ses interprétations. Bulletin mycologique et botanique Dauphiné-Savoie: 165–174.

Van Vooren N. 2011b. Premiers signalements d'Otidea caligata (Nyl.) Sacc. (Ascomycota, Pezizales) en France. Ascomycete.org 3: 61–64.

Van Vooren N, Armada F. 2011. Redécouverte d'Otidea platyspora Nannf. (Ascomycota, Pezizales) en France. Bulletin mycologique et botanique Dauphiné-Savoie 203: 57–62.

Van Vooren N, Carbone M. 2012. The genus Otidea. VI. Otidea felina and its interpretations. Ascomycete.org 4: 29–34.

Van Vooren N, Hairaud M, Jindřich O. 2008. Otidea tuomikoskii, Otidea papillata et Otidea papillata f. pallidefurfuracea f. nov. trois taxons remarquables appartenant au genre Otidea (Pezizales, Pyronemataceae). Bulletin mycologique et botanique Dauphiné-Savoie 188: 47–57.

Van Vooren N, Olariaga I, Tabarés M. 2011. First record of Otidea caeruleopruinosa Harmaja (Ascomycota, Pezizales) in the Iberian Peninsula. Ascomycete.org 3: 43–46.

Yao Y-J, Spooner BM. 2006. Species of Sowerbyella in the British Isles, with validation of Pseudoombrophila sect. Nannfeldtiella (Pezizales). Fungal Diversity 22: 267–279.

Zhuang WY. 2006 '2005'. Notes on Otidea from Xinjiang, China. Mycotaxon 94: 365–370.

Zhuang WY. 2010. Taxonomic assessment of some pyronemataceous fungi from China. Mycotaxon 112: 31–46.

Zhuang WY, Korf RP. 1987. Some new species and new records of discomycetes in China. II. Mycotaxon 29: 309–314.

Zhuang WY, Korf RP. 1989. Some new species and new records of discomycetes in China. III. Mycotaxon 35: 297–312.

Zhuang WY, Yang ZL. 2008 '2007'. Some pezizalean fungi from alpine areas of southwestern China. Mycologia Montenegrina 10: 235–249.

INDEX to species, varieties and forms

Accepted names treated in the monograph are in ***bolditalic***.