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Source: Integrative Systematics: Stuttgart Contributions to Natural History, 6(2) : 1-37

Published By: Stuttgart State Museum of Natural History

URL: https://doi.org/10.18476/2023.787646

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Integrative Systematics 6 (2): 1–37; published online 30.XII.2023; DOI: 10.18476/2023.787646

RESEARCH ARTICLE

Three new smooth-spored species of *Inocybe*, two new epitypes, and updates on earlier epitypifications

Ditte Bandini[1*], Giovanni Bandini[1], Konstanze Bensch[2], Francisco J. Rodríguez Campo[3],
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Abstract

Three new smooth-spored species of *Inocybe* are described based on detailed morphological and molecular investigation: *Inocybe bonii*, *I. carolina* and *I. centesima*. The new species are presented with a detailed description, macroscopic and microscopic photographs, as well as drawings of microscopic details. For two species, *I. albomarginata* and *I. rufuloides*, epitypes were selected, and a description and a figure plate of each of them are provided. Furthermore, a portrait of *I. amblyospora* is given, a species that has often been confused with *I. albomarginata*. Based on our studies, we affirm that *I. reducta* and *I. albomarginata* are synonymous. All named species are supported by phylogenetic analyses. Lectotypifications that were missing so far (*I. geophylla*, *I. hirtella*, *I. tigrina* and *I. transitoria*) are now supplied. The typification information is amended for *I. tarda* and corrected for *I. griseovelata*.

Keywords: *Agaricales*, *Inocybaceae*, molecular systematics, nrITS, nrLSU, alpha taxonomy, type studies, epitype.

Zusammenfassung

Auf der Basis detaillierter morphologischer und molekularer Untersuchungen werden drei neue glattsporige Arten von *Inocybe* beschrieben: *Inocybe bonii*, *I. carolina* und *I. centesima*. Die neuen Arten werden mit ausführlicher Beschreibung, makroskopischen und mikroskopischen Fotos sowie Zeichnungen der mikroskopischen Details präsentiert. Für zwei Arten, *I. albomarginata* und *I. rufuloides,* wurden Epitypen gewählt und jeweils eine ausführliche Beschreibung und eine Tafel angefertigt. Außerdem wurde ein weiteres Porträt einer Art gegeben, die oft mit *I. albomarginata* verwechselt wurde und wird: *Inocybe amblyospora*. Basierend auf unseren Studien bestätigen wir die Synonymie von *I. reducta* und *I. albomarginata*. Alle genannten Arten werden durch phylogenetische Analysen gestützt. Fehlende Lektotypifizierungen für *I. geophylla*, *I. hirtella*, *I. tigrina* und *I. transitoria* werden nachgeholt. Die Angaben zur Typifizierung von *I. tarda* werden ergänzt und für *I. griseovelata* berichtigt.

Introduction

The three species described here as new belong to the genus *Inocybe*, which is the largest of the seven genera in the family Inocybaceae (Matheny et al. 2020). The genus continues to grow, with several new species described from all over the world almost on a monthly basis. In the last five years alone, about 150 new species, all of them sequenced, have been published (e.g., Larsson et al. 2018a, 2018b; Matheny & Swenie 2018; Bandini et al. 2019a, 2019b, 2019c; Cripps et al. 2019b; Matheny & Kudzma 2019; Bandini et al. 2020a, 2020b, 2020c; 2021a, 2021b, 2021c; Cervini 2021; Crous et al. 2021; Dovana et al. 2021; Marchetti et al. 2021; Mešić et al. 2021; Bandini et al. 2022a, 2022b, 2022c; Crous et al. 2022; He et al. 2022; Bandini et al. 2023; Pošta et al. 2023; Rodríguez-Campo et al. 2023). Given that there are many parts of the world, for instance China, where there are no reliable estimates of the actual number of species (see, e.g., Fan & Bau 2010, 2013, 2020; Fan et al. 2018), and given the number of species in the databases, the total number of species is much higher (see Bhunjun et al. 2022).

The genus *Inocybe* s. str. is characterized, e.g., by the mostly thick-walled cheilocystidia and also mostly thick-walled pleurocystidia. Species with this combination of characters do not occur in the other six genera of the family (Matheny et al. 2020). The genus can be further divided into species that have either no metuloid caulocystidia or metuloid caulocystidia only near the apex, and those that have metuloid caulocystidia on the entire length of the stipe—usually visible as a fine pruina with the naked eye or with a magnifying glass. Whereas there are many species that have a distinctly pruinose stipe only near the apex, such as for instance species of the *I. flocculosa* or *I. cincinnata* groups, there are others that always have a distinctly pruinose stipe over its entire length, such as *I. subbrunnea* Kühner or *I. hirtella* Bres. However, there are other species whose stipe is variable from pru-

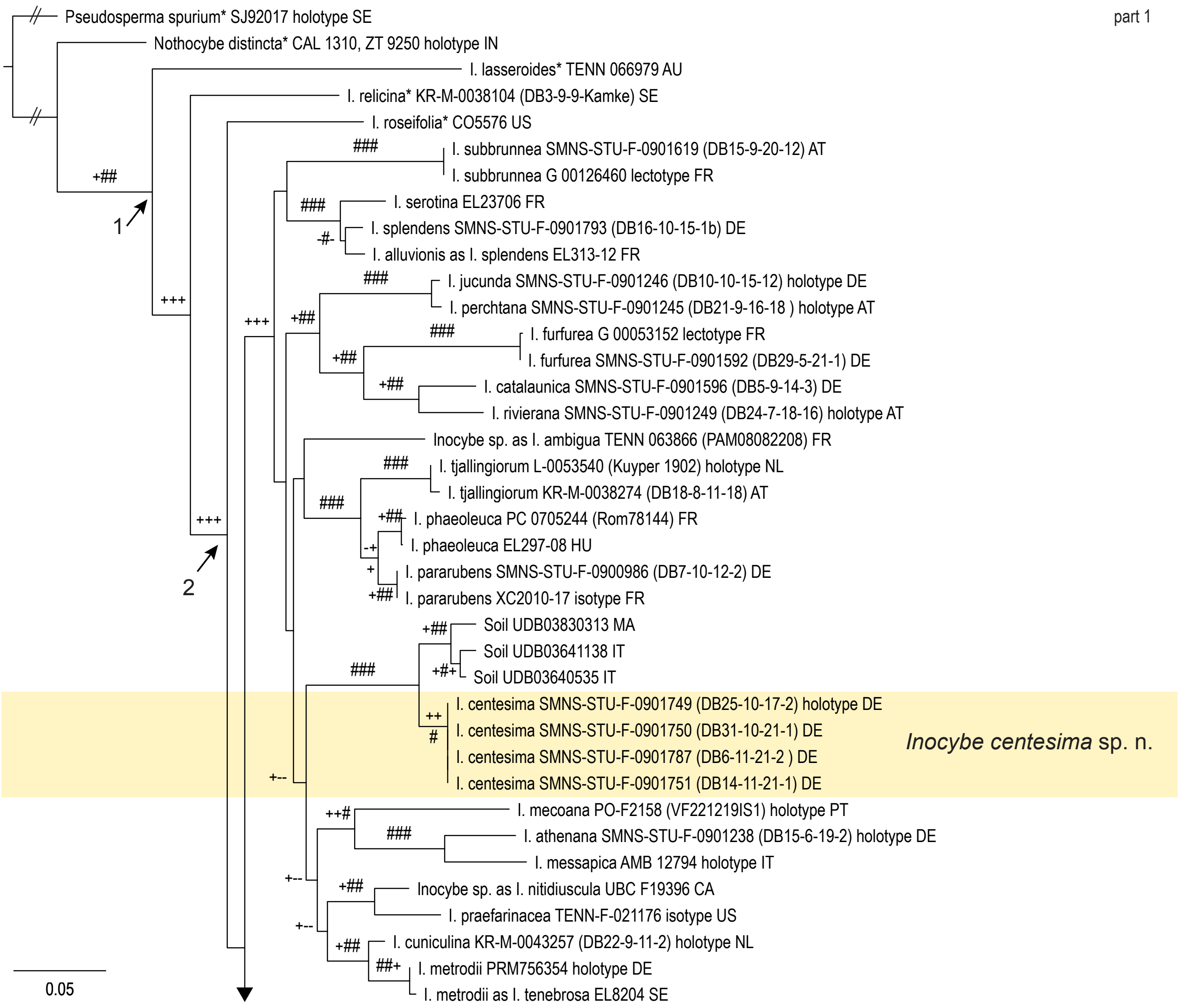

Fig. 1. ML topology resulting from analysis of combined ITS and partial LSU sequences of *Inocybe* treated or discussed here. Clades of species that are described here as new are highlighted in yellow; species clades for which type material is described here are highlighted in blue. Sequences taken from Matheny et al. (2020) are indicated by *. Arrow 1: *Inocybe* (genus), arrow 2: "smooth-spored temperate boreal clade" (Matheny et al. 2020). Support values from 5,000 replicates of SH-like approximate likelihood ratio test (SH-aLRT) support, 5,000 replicates of ultrafast bootstrap (ufb), and BI posterior probabilies (pp) indicated at the branches in this order. # indicating 100% or 1 support, + indicating values ≥ 80% SH-aLRT, ≥ 95% ufb or ≥ 0.95 pp.

inose only near the apex or down to the middle, or over its entire length; among the best-known examples of these are *I. sindonia* (Fr.) P. Karst. (see Kuyper 1986; Bandini et al. 2022b) and *I. nitidiuscula* (Britzelm.) Lapl. (DB, personal observation). There are also species whose stipe is pruinose over its entire length but in the lower half sometimes rather sparsely so. Thus, at first glance, the stipes of some basidiomata of these species seem to be pruinose only near the apex. This is the case, e.g., with the recently described *I. beatifica* Bandini & B. Oertel (Bandini et al. 2021c) or *I. jucunda* Bandini, B. Oertel & U. Eberh. (Bandini et al. 2021a).

We included in this article species from three of the above-listed groups: the stipe of *I. carolina* is pruinose always only near the apex, the stipe of *I. bonii* is pruinose over its entire length but sometimes only sparsely so in the lower half, possibly giving the impression that the stipe is pruinose only near the apex, while the stipe of *I. centesima* is always distinctly pruinose along its entire length—at least when young. With age, caulocystidia may be rubbed

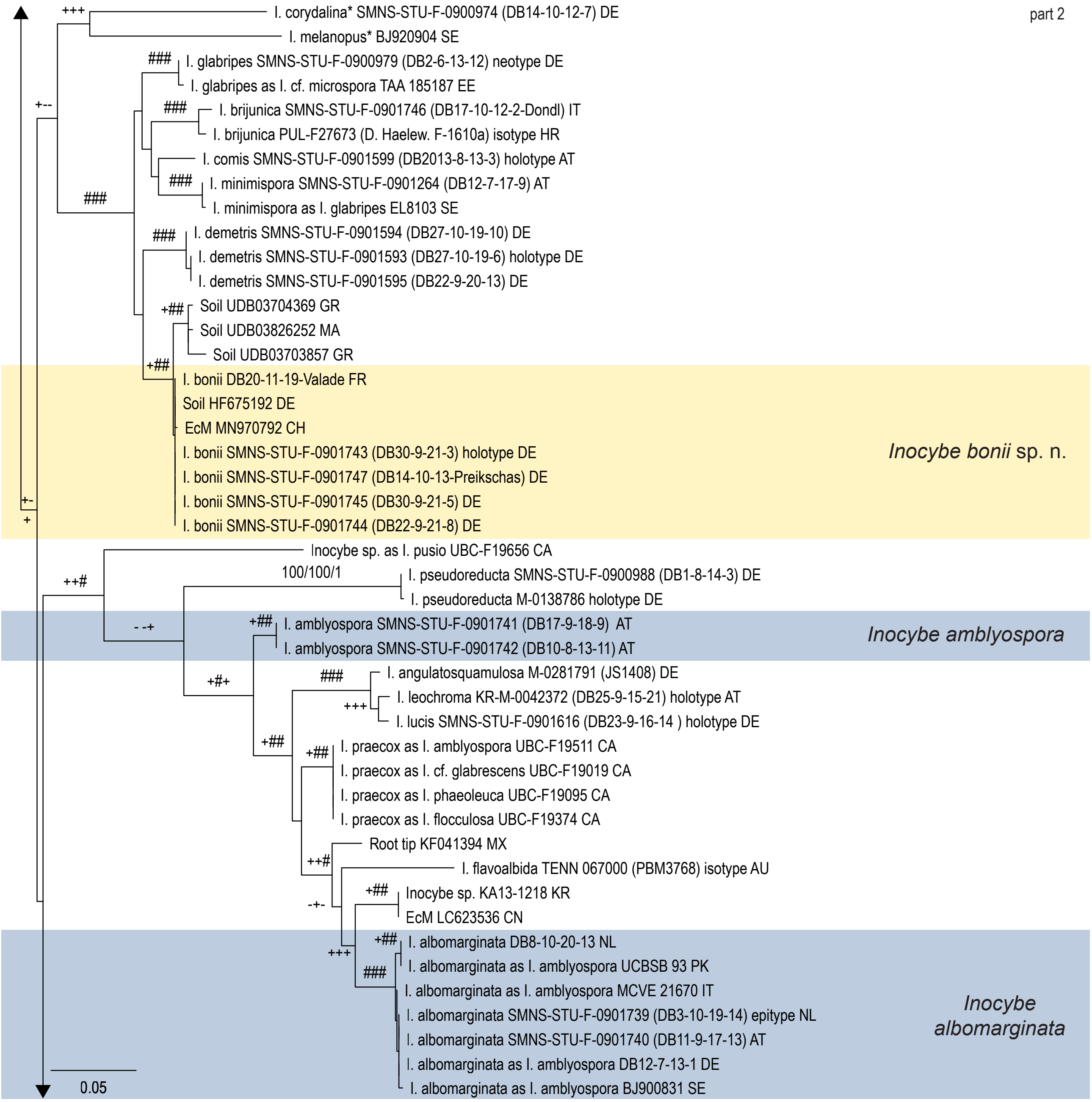

Fig. 1 (cont.)

off in the lower half of the stipe by adhering sand particles. The extent of pruinosity is a crucial question in keys (Kuyper 1986; Stangl 1989; Bon 1997a, 1997b, 1998), and is therefore of importance in the determination of species of the genus *Inocybe*.

Inocybe bonii has rather small spores and thus compares to other species with an entirely pruinose stipe and small spores, such as *I. albomarginata* Velen., *I. amblyospora* Kühner and *I. pseudoreducta* Stangl & Glowinski. In the past, these three species have sometimes been confused [see for instance the synonymization of *I. pseudoreducta* with *I. albomarginata* in Ludwig (2017)]. We have studied the types of *I. albomarginata* and *I. amblyospora*. In order to give a clearer picture of these species, we included below complete morphological descriptions for each of them.

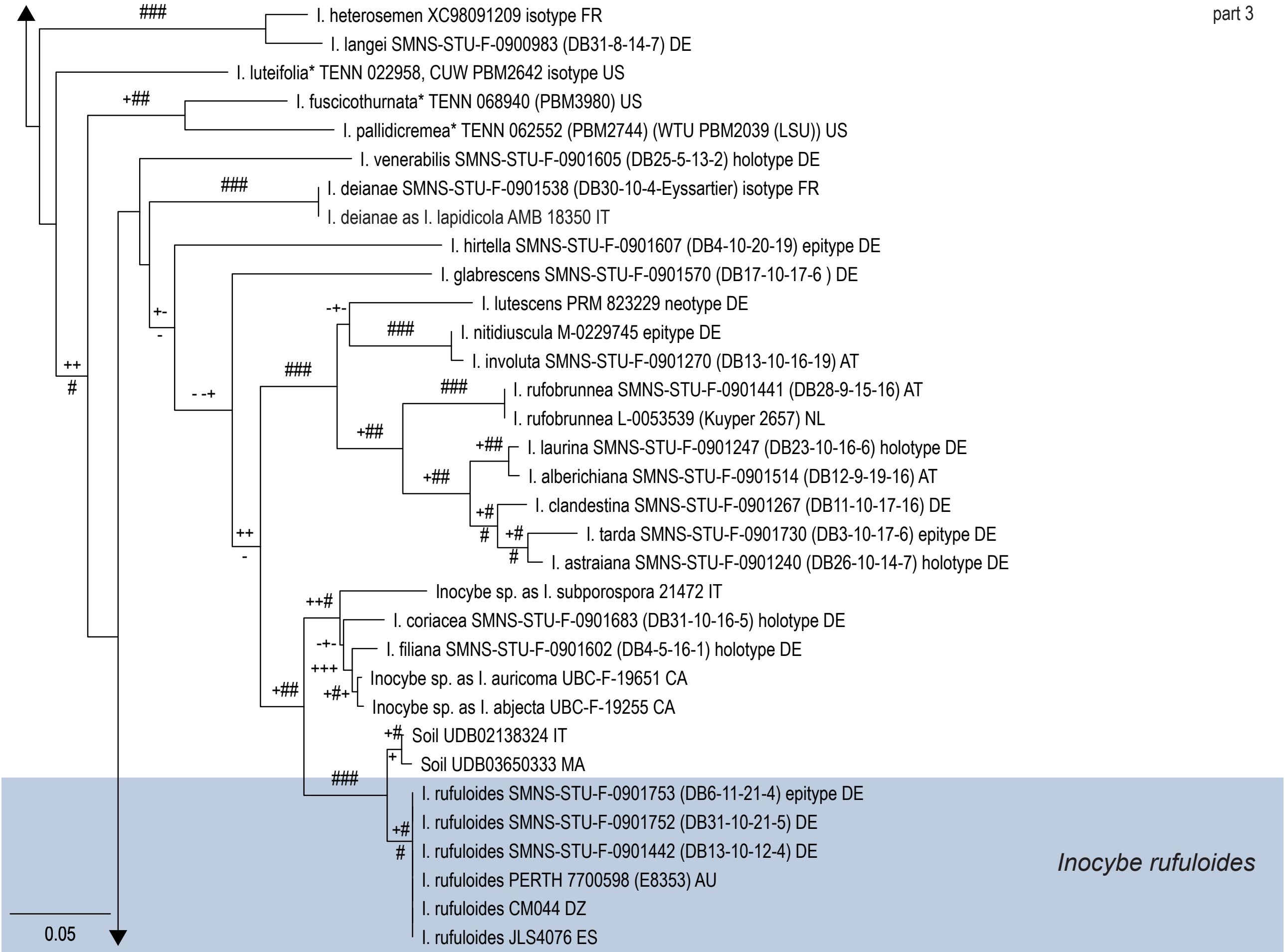

Fig. 1 (cont.)

All three species described here as new grow on calcareous soil: The holotype of *I. carolina* was found in an old limestone quarry near Madrid in Spain, and the paratypes of the species from Austria stemmed from a calcareous pebbled terrain on the border of a road near the river Lech. Both habitats are extremely dry and hot at times because of being exposed to the sun. The holotype and one paratype of *I. bonii* (see below) were found on the Swabian Jura in Germany, a mountain range the geology of which is mostly limestone from the Jurassic period with dry soil conditions, and *I. centesima* was found on an inland shell limestone sand dune originating from the last glacial period. Even in its current circumscription (Matheny et al. 2020), *Inocybe* is a genus that includes species that are rather divergent in their nuclear ribosomal genes. A satisfactory, comprehensive modern infrageneric classification based on phylogeny has not been reached so far. Thus, we continue to refer to Bon's (1997a, 1997b, 1998) classification as a guide through this large genus, even if it does not include any southern hemisphere *Inocybe*.

The selection of taxa considered in the analyses was largely driven by the species mentioned here, enriched with taxa used by Matheny et al. (2020) to delimit the genus. Although the molecular infrageneric classification of the genus remains a challenge, in our experience, good morphologically distinguishable *Inocybe* species do not share the same ITS sequence with other species of *Inocybe* [see Marchetti et al. (2021) for a diverging opinion based, however, on data from other genera, e.g., *Hebeloma*, *Cortinarius* and *Pluteus*].

Species delimitation followed the same principles used in earlier publications (Bandini et al. 2021c, 2022b), namely that species are described as new if they differ from existing species by the combination of at least three independent characteristics that are constant among representatives of the new species, and the representatives of the new species are monophyletic in phylogenetic ITS

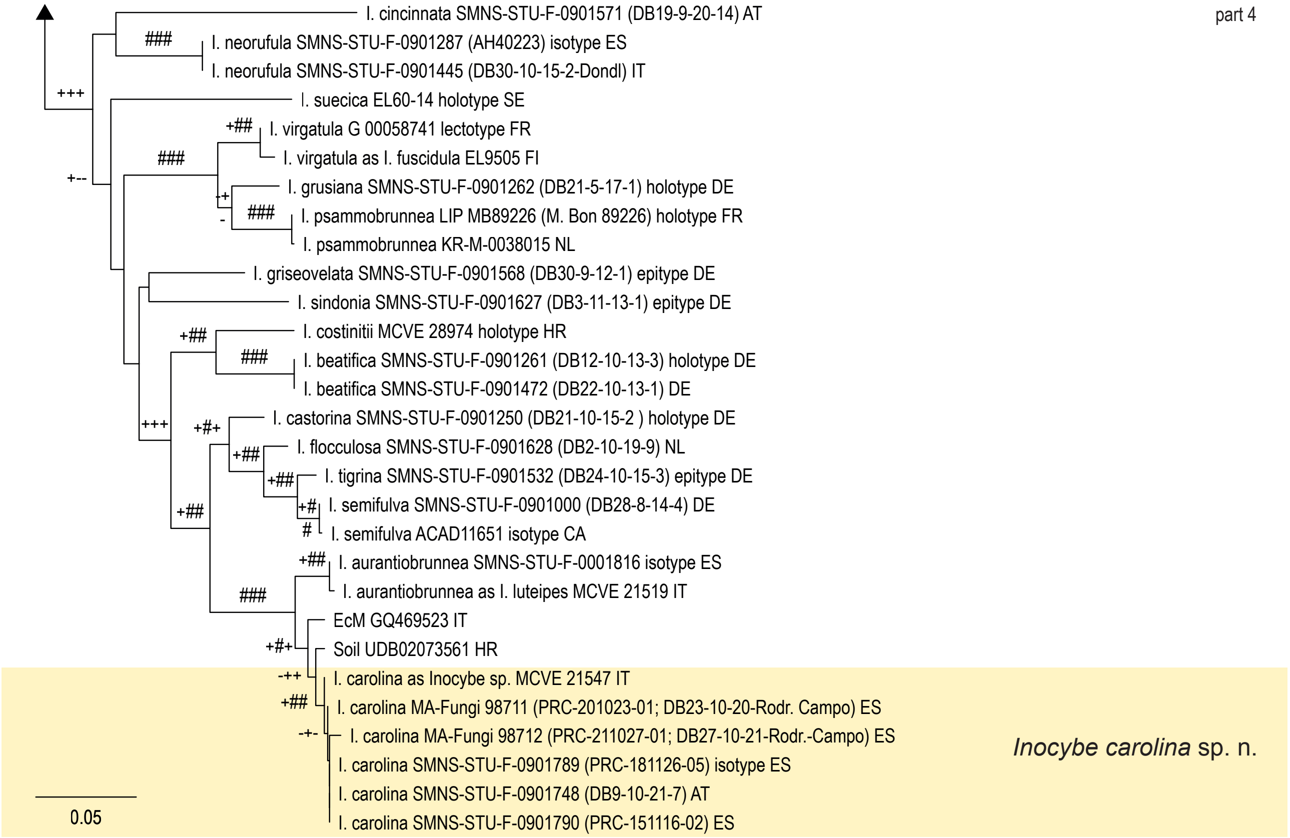

Fig. 1 (cont.)

(ITS + LSU) analyses. Constant ecological differences between new and existing species are considered as meaningful, but neither ecological nor ITS differences were used unless supported by morphological differences. Taxa were considered as synonymous if the overall impression of the species was very similar, if no constant characteristics could be found that separated the two species, and if neither pronounced ecological preferences nor molecular data (if available) indicated that the two species might be different (Bandini et al. 2021c).

Already in earlier publications (Bandini et al. 2021a, 2022a, 2022b), we began to designate epitypes in cases where the appraisal of the status of more recent names required the clarification of old names and the existing types did not show sufficient characters for species distinction. Important characters for species identification and delimitation that are often not observable in old material and not explicitly mentioned in species descriptions are associated with the caulocystidia at the top of the stipe. The features of the caulocystidia directly below the lamellae form a character that we started to use relatively recently (Bandini et al. 2017) but that we have since found to be very useful for species recognition in *Inocybe*. Here, we decided to select epitypes for *I. albomarginata* and *I. rufuloides*. The holotype of *I. albomarginata* is immersed in formaldehyde and therefore almost an amorphous mass, making it impossible to study the caulocystidia; moreover, it is preserved in a bottle together with several other species of other genera. The holotype of *I. rufuloides*, a species growing alongside *I. centesima* in good years, has defied sequencing attempts by several experts. Moreover, the material is in bad condition so that not all microscopic characters important for differentiation from other species could be determined, such as, e.g., the often catenate, often slightly thick-walled paracystidia or caulocystidia directly below the lamellae.

We furthermore supplied lectotypes for *I. geophylla*, *I. hirtella*, *I. tigrina* and *I. transitoria* that ought to have been assigned earlier, when these taxa were epitypified. For old taxa, it is often difficult to know whether syntypes exist. Epitypes only serve as interpretative types for the material that is cited in the epitypification and not for syntypes. Lectotypification is necessary to preclude the occurrence of competing epitypes. We also used the opportunity to amend the typification information for *I. tarda* and correct it for *I. griseovelata*.

Fig. 2. *Inocybe albomarginata*. **a**. Epitype, scale bar: 1 cm. **b**. Coll. DB21-10-13-1, scale bar: 1 cm. **c**. Cheilocystidium (coll. DB1-6-13-19), scale bar: 10 µm. **d**. Microscopic characters (epitype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e**. Spores (coll. DB1-6-13-19), scale bar: 10 µm.

Material and methods

Morphological study

Fresh materials were obtained on forays in Austria, France, Germany and Spain between 2017 and 2021. For fresh collections, the relevant macroscopic details, i.e., habit, size and shape of the basidiomata, colour and surface of the pileus, number and colour of the lamellae, size, colour, surface and base of the stipe, smell and colour of the flesh, colour of the exsiccata, habitat and surrounding trees, were noted.

For all collections—if possible in the fresh, otherwise in the dried state—basidia, spores, hymenial cystidia, caulocystidia etc. were examined by D. Bandini with a Leica DM-750 microscope, in water and in a 3% KOH solution, at 400× and 1,000× magnifications. Photographs of microscopic details were taken by D. Bandini with a Zeiss AxioCam ERc5s. The measurements of spores and cystidia were determined using Zeiss Axiovision version 4.8. Cystidia were measured without crystals and basidia without sterigmata. The size of all elements measured is given as length × width. The Q value equals the ratio of spore length to spore width (calculated for each spore). The number of spores or cystidia measured is included in the descriptions.

The macroscopic photographs of *I. carolina* (Fig. 5a, b) were taken by F. J. Rodríguez Campo with a Nikon D300S with Micro-Nikkor 105 mm lens, and the photograph in Fig. 4b of *I. bonii* was taken by F. Valade with a Canon EOS 80D + 60 mm macro lens. All other macrophotographs were taken by D. Bandini with a Panasonic Lumix GH2 with Leica DG Macro-Elmarit 1:2.8/45 mm lens. For the determination of colour temperature, a calibration card was photographed together with the fresh collections at the collection site. The RAW files were developed with Silkypix Developer Studio 4.0.

All drawings of microscopic details were done by D. Bandini. Colour codes were taken from Munsell (2009, as "Mu"); terminology follows Vellinga (1988) and Kuyper (1986). Herbarium acronyms are according to Holmgren et al. (1990); D.B./DB refers to the private herbarium of Ditte Bandini, PRC to the private herbarium of F.J. Rodríguez Campo, and FV to the private herbarium of F. Valade.

Molecular study

DNA extraction, PCR and sequencing of nrDNA ITS and LSU followed the protocols published by Cripps et al. (2019a) and Bandini et al. (2021c). For epitypes and other material processed in Stuttgart, DNA extracts are available at the Staatliches Museum für Naturkunde Stuttgart (Germany, SMNS) for the generation of sequences from other DNA regions as needed. Bidirectional sequencing was carried out by LGC Genomics (Berlin, Germany). Sequence editing and assembly were done in Sequencher v. 4.9 (Genecodes). Newly generated sequences were submitted to GenBank with acc. no. OR102467–OR102487. The new sequence with GenBank acc. no. OQ546722 was generated in the CEFE lab in Montpellier (France), the sequences with GenBank acc. no OR100607, OR100705, OR102492 and OR102493 were generated by Alvalab (Oviedo, Spain).

Sequences were blasted against GenBank (Johnson et al. 2008) and in Geneious R10 (Biomatters) against the "Full "UNITE+INSD" dataset" (Abarenkov et al. 2022), in order to find additional records for the species treated here and putative close relatives. The majority of the close relatives were found among taxa treated in earlier publications (Bandini et al. 2021c, 2022a, 2022b; Vauras & Larsson 2016), so that for each species, the inclusion of a single full-length sequence (ITS + LSU approx. 1400 bp) or the type sequence plus one full length sequence, if available, was considered sufficient. Only for direct sister species of any of the target species three sequences were included. For every species [or species hypothesis—see Kõljalg et al. (2005)] included, we selected one to three representative sequences for the tree analyses by length (inclusion of LSU), quality and preferred, if available, sequences from types and studied material, i.e., from other molecular systematic studies, preferentially selecting basidiome over EcM or root tip sequences, and the latter over soil sample data.

Sequence similarity or identity values were directly copied from BLAST results. Percent values given in the text refer to ITS1-5.8S-ITS2 or fewer positions if the complete sequence was unavailable for at least one of the sequences. Conspecificity between public sequences and sequences of types was assumed if sequence variation was 1% or less. This value was selected to be smaller than the 98.5% cut-off value proposed by several authors (Lücking et al. 2020 and references therein), to be used as general cut-off values for ITS variation to distinguish between species. Sequence variation attributed to long indels, stretches of N (i.e., in cases in which the ITS was obtained in two amplicons, not allowing to read the entire ITS) or obviously wrong sequence reads in the beginnings or ends of published sequences were ignored. Information on distribution beyond the information from our own data was obtained from UNITE species hypotheses (sh) v. 9.0 (Kõljalg et al. 2013; Abarenkov et al. 2022). Correspondence of species with UNITE sh was assumed if the query sequence had a 100% or 99.7% matching sequence present in the sh.

For species described as new, we aimed at having at least three collections sequenced for ITS and LSU, provided sufficiently many collections were available for sequencing. Representatives of published sequences from collections putatively belonging to these taxa or very close relatives of these taxa (i.e., > 97% similar in BLAST results) were also included.

The alignment was carried out in MAFFT v. 7 using the E-INS-i option (Katoh et al. 2005, 2019), adding the ITS and LSU sequences considered by Matheny et al. (2020) for defining *Inocybe* to our own dataset to create a backbone for the tree. *Pseudosperma spurium* (Jacobsson & E. Larss.) Matheny & Esteve-Rav. was used for rooting.

The entire alignment was treated as a single partition. All positions were included in the analysis. ML analyses were run in IQ-TREE v. 1.6 (Nguyen et al. 2015) online (Trifinopoulos et al. 2016), with standard settings. Branch support was obtained through 5,000 replicates of UFBoot (Minh et al. 2013; Hoang et al. 2018) and SH-aLRT (Guindon et al. 2010).

Bayesian inference (BI) was done in MrBayes 3.2.7a (Ronquist et al. 2012) using BEAGLE (Ayres et al. 2012) on CIPRES (Miller et al. 2010). The BI analysis was carried out in two runs with four chains including one heated chain each, using the GTRINVGAMMA model, default priors and sampling one tree of each run every 1,000 generations. The analysis stopped employing default stop rule parameters after 2.005 million generations (Ronquist et al. 2020). The first 25% of trees were discarded as burn-in.

The tree was visualized using FigTree v. 1.4.4 (Rambaut 2006–2018). Support values were noted as SH-aLRT support [%], ultrafast bootstrap (ufb) support [%] and BI posterior probability (pp). SH-aLRT support ≥ 80%, ufb support ≥ 95% and pp ≥ 0.95 are indicated at the branches. Alignment and tree files are available in TreeBASE at http://purl.org/phylo/treebase/phylows/study/TB2:S30548.

Fig. 3. *Inocybe amblyospora*. **a**. Coll. DB17-9-18-9, scale bar: 1 cm. **b**. Coll. DB20-8-12-12, scale bar: 1 cm. **c**. Cheilocystidia (coll. DB20-8-12-12), scale bar: 10 µm. **d**. Microscopic characters (coll. DB17-9-18-9); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e**. Spores (coll. DB20-8-12-12), scale bar: 10 µm.

Specimen depositories

Herbarium acronyms are according to Holmgren et al. (1990) except D.B., which refers to the private herbarium of Ditte Bandini.

Results

In the taxonomy section, all species are listed that are either newly described, newly typified or for which earlier typifications are updated.

The molecular results are shown in Fig. 1. All of the species discussed in detail in this paper are supported as members of the genus *Inocybe* and belonging to the "smooth-spored temperate boreal clade", here receiving 88/96/0.96 support, as defined by Matheny et al. (2020).

Sequences included in the phylogenetic analyses (Fig. 1) are listed in Appendix 1. The final alignment included 145 sequences and 2,314 positions. The result of the ML analysis is depicted in Fig. 1. The consensus tree resulting from the BI analysis was generally similar to the ML result and differed only in clades not supported in either of the analyses.

The clade including *I. bonii* and a supported clade of soil sequences (that form a clade with 97/100/1 support) received 99/100/1 support. The sequences known to represent *I. bonii* morphologically (plus two non-specimen derived sequences) and highlighted as *I. bonii* in Fig. 1 (part 2) form a hardly diverging unsupported clade, sister to the above-mentioned soil sequences clade. Sequences of *I. carolina* s. l. form a clade that received 85/100/0.96 support (Fig. 1, part 4). The clade of *I. carolina* s. str. (indicated as *I. carolina* in Fig. 1) received 89/100/1 support. The sequences of *I. centesima* form a clade with 94/99/1 support; the sister clade consisting of soil sequences is also well supported (96/100/1) and likely represents an unknown taxon. *Inocybe rufuloides* sequences form a clade with 97/100/1 support (Fig. 1, part 3). The *I. rufuloides* species clade has a sister clade (84/100/0.97) consisting of soil sequences that are considered to represent a different taxon. What we here consider as *I. amblyospora* (clade support 87/100/1) is phylogenetically related to *I. albomarginata* (clade support 100/100/1); the two species are resolved within the same clade together with, e.g., *I. angulatosquamulosa* and *I. flavoalbida*, but not as direct sister species (Fig. 1, part 2).

The only supported clade (Fig. 1, part 1) within this tree that included *I. centesima* and other named species (with 94/99/0.97 support, from *I. subbrunnea* down to *I. metrodii*) encompassed species such as *I. splendens*, *I. phaeoleuca* and *I. furfurea*. The position of *I. centesima* within this clade is unresolved, i.e., its phylogeny is unsupported in relation to named species. *Inocybe bonii* is supported in a clade with *I. glabripes* (100/100/1 support) (Fig. 1, part 2). *Inocybe albomarginata* and *I. amblyospora* were included in the same clade, with 98/100/1 support; the entire clade also included *I. pseudoreducta* and an unnamed species (represented by UBC-F19656) and received 96/99/1 support (Fig. 1, part 2). *Inocybe carolina* (Fig. 1, part 4) was included in a clade with, e.g., *I. flocculosa* (support 98.100/1); the entire clade from *I. cinncinata* down to *I. carolina* received 96/99/0.98 support. *Inocybe rufuloides* (Fig. 1, part 3) was well supported (97/100/1) within a group of species including *I. coriacea* Bandini, B. Oertel & U. Eberh., *I. filiana* Bandini, B. Oertel & U. Eberh. and a number of sequences of unknown species, but following the support towards the backbone of the tree, support especially from SH-aLRT was rather low in some cases. Support from ufb suggested a relationship with, e.g., *I. tarda* (81/98/-), whereas support from pp with *I. glabrescens*.

Taxonomy

Inocybe albomarginata Velen., *České* Houby 2: 379 (1920) (Figs. 2, 8a, c)

Heterotypic synonym: *Inocybe reducta* J.E. Lange, Fl. Agaric. Danic. 5(Taxon. Consp.): V, 101 (1940).

Selected description and iconography: Velenovský (1920–1922); Lange (1940, as "*I. reducta*"); Kuyper (1986); Stangl (1989).

Typification

Lectotype designated by Kuyper (1985: 376): CZECH REPUBLIC, Prag, Mnichovice, in Betuletum above railway (viam ferream), Aug. 1915 [leg. J. Velenovský] (PRC-bottle n°119).

Epitype (designated here; MBT 10014037)

NETHERLANDS, Drenthe, Assen, park of hospital, alt. 15 m, *Quercus robur*, 3 Oct. 2019, leg. D. Bandini & E. Arnolds (STU SMNS-STU-F-0901739; dupl. priv. herb. DB DB3-10-19-14).

Description

Pileus 20–45 mm wide, (sub)globose or subcampanulate when young, later broadly convex or expanded, often somewhat deformed, with or without a low, large umbo, margin at first slightly to strongly inflexed, later decurved and with age straight to even uplifted, and then depressed around the centre; no remnants of a velipellis observed; colour mostly brown with reddish to red-brown hue (Mu 7.5YR 4/4–4/6, 5/4–5/8), rarely somewhat paler and with ochraceous tinge (Mu 10YR 5/4–5/8), sometimes darker to almost blackish brown at the centre and often somewhat speckled with fine darker fibre bundles on paler ones, margin sometimes much paler with age; surface at first glabrous, then finely innately fibrillose to rimulose near the margin, but often also strongly rimose with fibres diverging and showing the lighter-coloured context beneath; when aging at the centre, usually areolate-diffracted or somewhat cracked or "scabby" or breaking

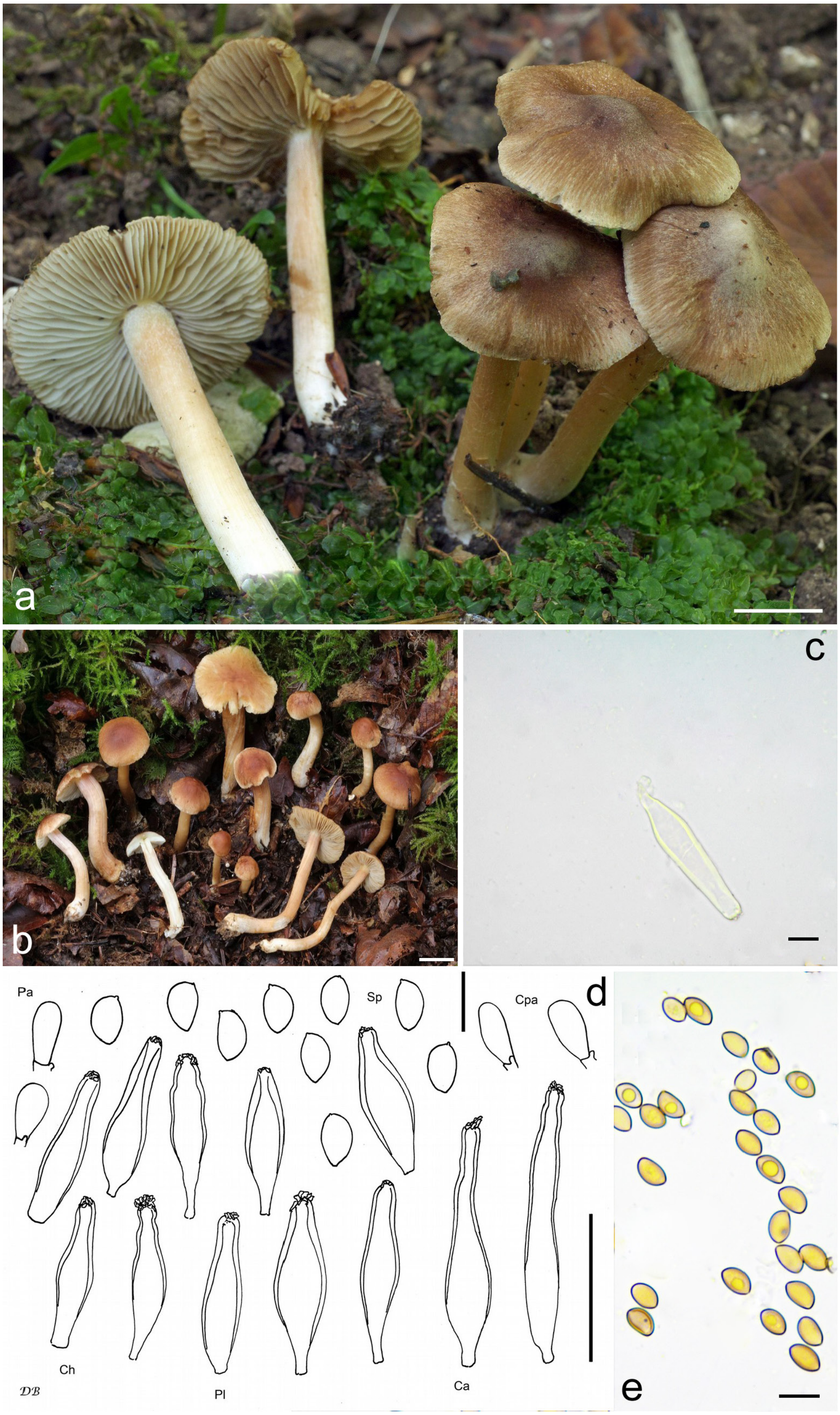

Fig. 4. *Inocybe bonii*. **a**. Holotype, scale bar: 1 cm. **b**. Coll. DB20-11-19-Valade (photo F. VALADE), scale bar: 1 cm. **c**. Cheilocystidium (holotype), scale bar: 10 µm. **d**. Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e**. Spores (holotype), scale bar: 10 µm.

up in small particles; no cortina observed. *Lamellae* moderately crowded [c. 40–50 (60), l = 1–3], often uneven, slightly thick, adnexed to adnate, usually very flat, even to subventricose, at first whitish, later beige to pale ochraceous; edge whitish. *Stipe* 30–60 × 2–6 mm, straight or curved and often widening towards the base, base usually thickened to (sub)bulbous, sometimes with a rather thick bulb (up to 10 mm), when young entirely covered with thin whitish tomentum, later longitudinally striate or glabrous, flesh-coloured to brown or reddish brown, up to dark reddish brown or red-brown with age; pruinose along entire length, but more densely so in the upper half of the stipe and sometimes seemingly only near the apex. *Context* whitish in the pileus, at first whitish in the stipe, with age brownish in the cortex and sometimes streakily brownish also in the stipe, base remaining whitish. *Smell* spermatic, at least when cut. *Colour of exsiccata*. Pileus brown to dark brown with reddish hue (Mu 5YR 4/4–4/6, 3/3–3/4), lamellae somewhat lighter, stipe concolorous or a little lighter, no darkening or blackening on drying.

Spores 5.9–9.5 µm (av. 7.3 µm, SD 0.7 µm) × 3.7–5.0 µm (av. 4.3 µm, SD 0.3 µm); Q = 1.4–2.1 (av. 1.7, SD 0.1) (n = 120 of 3 coll.), smooth, subamygdaloid, sometimes oblong, occasionally with a faint suprahilar depression, apex mostly subobtuse. *Basidia* 25–30 × 7–9 µm, generally 4-spored. *Pleurocystidia* 36–79 µm (av. 56 µm, SD 10 µm) × 11–24 µm (av. 15 µm, SD 3 µm); Q = 2.3–6.1 (av. 3.7, SD 1.0) (n = 45 of 3 coll.), mostly subfusiform to (sub)utriform, usually without or with only a short neck, at the apex generally wide, with a short pedicel, apex usually crystalliferous, mostly rather thin-walled and walls rather uniformly thick near bulge and apex, but with only few small crystals, walls up to 1.5 (2.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size, intermixed with colourless (sub)clavate, thin-walled paracystidia. *Pileipellis* constituted by an epicutis made up of parallel hyphae 4–11 µm wide, with finely encrusting and parietal brown pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* descending the entire length of the stipe but sometimes sparsely so on the lower half, 30–65 × 9–20 µm, mostly ventricose (sub)utriform or (sub)fusiform, sometimes deformed, without or with only a short neck and with a short pedicel, apex with or without small crystals; walls up to 0.5 (1.0) µm thick at the apex, pale yellowish-greenish with 3% KOH; intermixed with colourless, (sub)clavate, thin-walled cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe albomarginata was found by us with frondose trees, often in park-like terrain on calcareous soil. Judging from the collection data, the species appears to often associate with *Quercus*. Our own collections are from Austria, Germany and The Netherlands. The corresponding species hypothesis (SH0740134.09FU, 2.0 %) includes sequences from Czechia, Estonia, Finland, Germany, Italy, Latvia, The Netherlands, Pakistan, Russia, Sweden and Turkey. The species seems to be widespread, ranging from Europe to south Asia and quite common.

Type specimens examined

Lectotype of *I. albomarginata* (PRC-bottle n°119) (Fig. 8a): *Spores* 6.4–7.8 µm (av. 7.1 µm, SD 0.3 µm) × 3.8–4.5 µm (av. 4.2 µm, SD 0.2 µm); Q = 1.6–1.9 (av. 1.7, SD 0.1) (n = 40), smooth, subamygdaloid, sometimes oblong, occasionally with a faint suprahilar depression, apex subobtuse. *Basidia* 4-spored. *Pleurocystidia* 32–58 µm (av. 46 µm, SD 7 µm) × 11–17 µm (av. 14 µm, SD 2 µm); Q = 2.5–5.2 (av. 3.3, SD 0.6) (n = 40)], mostly (sub)fusiform or (sub)utriform, apex usually crystalliferous, walls up to 1.0 (1.5) µm thick at the apex, yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* (sub)clavate, colourless, thin-walled. *Caulocystidia* not studied (because in a bad condition).

Syntype of *I. reducta* (Fig. 8c): DENMARK, Husmandskolen near Odense, Sep. 1938, [leg. J.E. Lange] (C-F-67157). *Spores* 6.5–8.0 µm (av. 7.2 µm, SD 0.3 µm) × 4.0–5.0 µm (av. 4.3 µm, SD 0.2 µm); Q = 1.5–1.8 (av. 1.6, SD 0.1) (n = 40), smooth, subamygdaloid, sometimes oblong, occasionally with a faint suprahilar depression, apex subobtuse. *Basidia* 4-spored. *Pleurocystidia* 44–57 µm (av. 51 µm, SD 5 µm) × 13–17 µm (av. 15 µm, SD 1 µm); Q = 2.9–3.8 (av. 3.4, SD 0.3) (n = 40), mostly (sub)fusiform or (sub)utriform, apex usually crystalliferous, walls up to 1.0 (1.5) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* (sub)clavate, colourless, thin-walled. *Caulocystidia* not studied (to preserve the material).

Epitype of *I. albomarginata* (Figs. 2a, d): *Spores* 6.2–9.1 µm (av. 7.2 µm, SD 0.5 µm) × 3.7–4.8 µm (av. 4.3 µm, SD 0.3 µm); Q = 1.4–1.9 (av. 1.6, SD 0.1) (n = 40), smooth, subamygdaloid, sometimes oblong, occasionally with a faint suprahilar depression, apex (sub)obtuse. *Basidia* 4-spored. *Pleurocystidia* 42–71 µm (av. 54 µm, SD 10 µm) × 13–17 µm (av. 14 µm, SD 1 µm); Q = 2.5–5.5 (av. 3.8, SD 0.9) (n = 40), mostly (sub)fusiform or (sub) utriform, apex usually crystalliferous, walls up to 1.5 (2.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* (sub) clavate, colourless, thin-walled. *Caulocystidia* on entire length of the stipe, 35–60 × 9–15 (20) µm, mostly ventricose (sub)utriform or (sub)fusiform.

Selected additional specimens examined

AUSTRIA, Tirol, Imst, Silz, ÖK25V 2221-Ost, alt. 660 m, riparian forest with *Tilia* sp., *Pinus sylvestris*, *Fraxinus* sp., *Populus* sp., 11 Sep. 2017, leg. D. Bandini (SMNS-STU-F-0901740, DB11-9-17-13). GERMANY, Baden-Württemberg, Karlsruhe, Erzbergerstr., TK25 6916/3, alt. 118 m, lawn with *Quercus petraea*, *Fagus sylvatica*, *Carpinus sylvaticus*, 1 Jun. 2013, leg. D. Bandini & B. Oertel (DB1-6-13-19). Nordrhein-Westfalen, Siegen-Wittgenstein, Freudenberg, Rest stop Siegerland, TK25 5013/3, *Fagus sylvatica*, *Corylus avellana*, 21 Oct. 2013, leg. D. Bandini (DB21-10-13-1). NETHERLANDS, Drenthe, Assen, park of hospital, alt. 15 m, *Quercus robur*, 3 Oct. 2019, leg. D. Bandini & E. Arnolds (DB3-10-19-14). Drenthe, Gijsselte, alt. 15 m, *Quercus robur*, 6 Oct. 2020, leg. D. Bandini (DB6-10-20-6). Drenthe, Diever, alt. 16 m, *Pinus sylvestris*, *Picea abies*, *Quercus robur*, *Fagus sylvatica*, 8 Oct. 2020, leg. D. Bandini

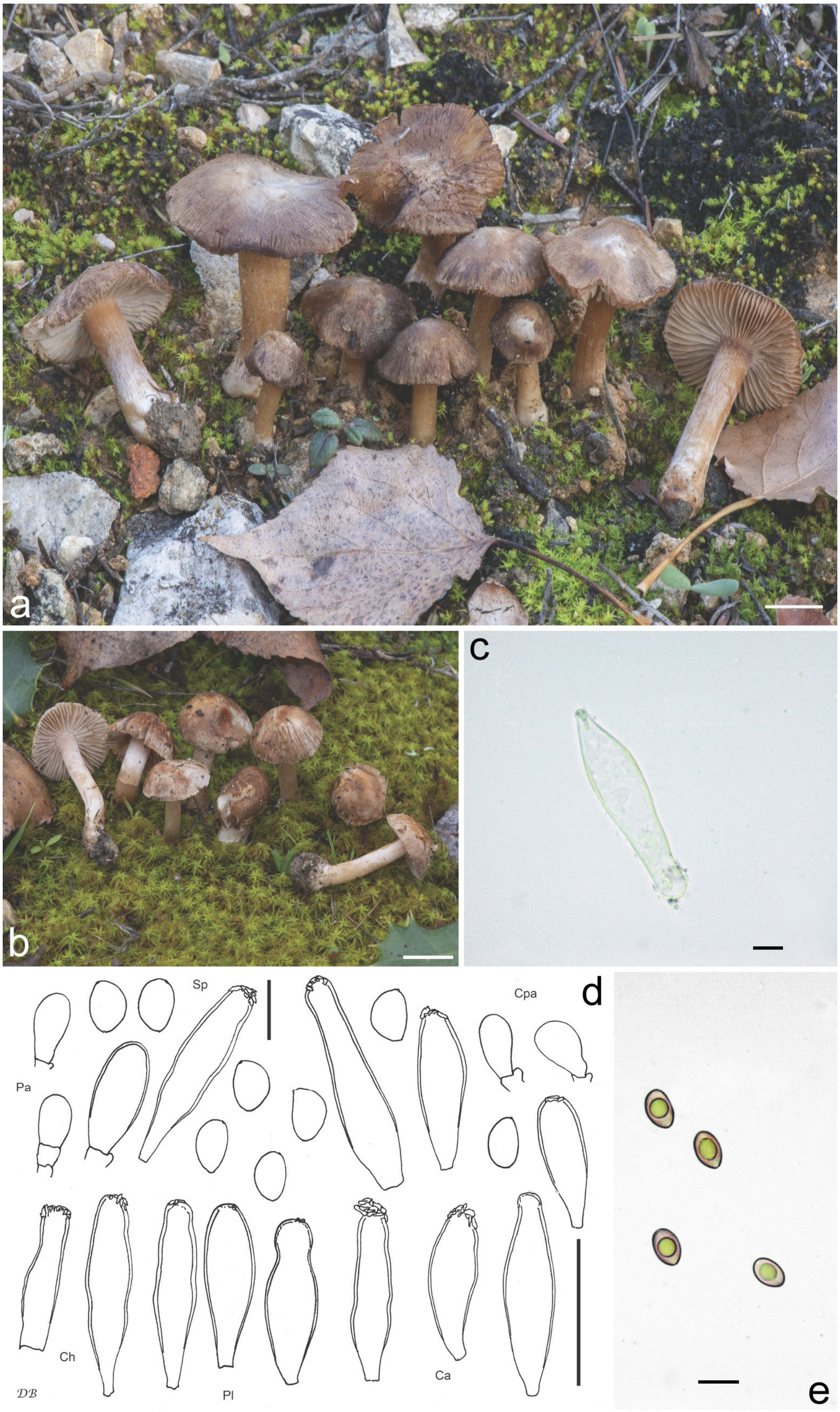

Fig. 5. *Inocybe carolina*. **a**. Holotype (photo: F.J. Rodríguez-Campo), scale bar: 1 cm. **b**. Coll. MA-Fungi 98711 (photo: F.J. Rodríguez-Campo), scale bar: 1 cm. **c**. Cheilocystidium (DB9-10-21-7), scale bar: 10 µm. **d**. Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e**. Spores (DB9-10-21-7), scale bar: 10 µm.

(DB8-10-20-1). Ibidem, alt. 15 m, *Pinus sylvestris*, *Picea abies*, *Quercus robur*, *Fagus sylvatica*, 8 Oct. 2020, leg. D. Bandini (DB8-10-20-13).

Notes

The lectotype of *I. albomarginata* is preserved in formaldehyde in a bottle together with samples of different genera (see also Kuyper 1985). The consistency of the fruiting bodies is soft and jelly-like and the lectotype is not in a good condition, so, e.g., the caulocystidia cannot be examined. There is no chance that caulocystidia will be observable on any other material in the bottle. Therefore, and because no drawing or detailed description nor a photograph are given in the original description, and because *I. albomarginata* is often mistaken for *I. amblyospora*, we decided to select an epitype for *I. albomarginata*.

What is termed above as "syntype" of *I. reducta* is the only type material with details matching the holotype we are aware of, but as Lange did not specify where the type was deposited and not all of his material is in C, we cannot be sure it is the only instance of the material. *Inocybe reducta* was already synonymized with *I. albomarginata* by Kuyper (1985, 1986). Our morphological study of the type material in C supports this. Both have the same on average very small and especially very narrow spores, which excludes a synonymy with either *I. amblyospora* (see below) or *I. pseudoreducta* [with wider, often (sub)ovoid, apple-seed-like spores], and the shape of the hymenial cystidia is very similar; molecular data are not available from the type of *I. reducta*, because it was preserved in formaldehyde for some time.

Macroscopically, the pileus of *I. albomarginata* is mostly of reddish brown to red-brown colour, with a darker to almost blackish brown centre, its surface is at most finely innately fibrillose to rimulose, the lamellae are flat, and the species is furthermore characterized by an entirely but in the lower half sometimes sparsely pruinose stipe with a thickened to bulbous base and, on average, rather short subfusiform to (sub)utriform hymenial cystidia with a wide neck. A velipellis is lacking. *Inocybe amblyospora*, with which *I. albomarginata* has been mistaken [among others by Bandini et al. (2019b; MH366616) and Ryberg et al. (2008; AM882908.2), differs, e.g., by the presence of a velipellis, smoother pileus centre, on average longer spores and a different ecology. It occurs in montane to subalpine regions, often in somewhat moist terrain. *Inocybe suecica* Vauras & E. Larss., another species with small spores, can be distinguished from *I. albomarginata*, e.g., by the presence of a velipellis, smoother pileus surface and glabrous centre of pileus, as well as larger spores (Vauras & Larsson 2016; DB, personal observation), and *I. pseudoreducta*, e.g., by the presence of a velipellis, smoother centre of pileus, and wider spores often shaped like apple seeds (Stangl & Glowinski 1981; La Rosa et al. 2017). *Inocybe bonii* (see below) differs from *I. albomarginata*, e.g., by the greyish velipellis, smoother pileus surface at the centre, not flat lamellae and larger spores. *Inocybe demetris* Bandini & U. Eberh. differs, e.g., by the abundant velipellis, paler pileus colour, smooth centre of pileus, on average larger spores and much longer caulocystidia, as well as growth with conifers (Bandini et al. 2022b). *Inocybe metrodii* Stangl & J. Veselský can be distinguished from *I. albomarginata*, e.g., by the often larger basidiomata, presence of a velipellis, smoother centre of pileus, lamellae and stipe often partly becoming yellowish when bruised, and on average larger spores (Stangl & Veselský 1979; Bandini et al. 2021c), and *I. glabrescens* Velen., e.g., by the generally less stout basidiomata, abundant velipellis, pileus colour without reddish tinge, and larger spores (Velenovský, 1920-1922; Bandini et al. 2021c). Apart from *I. amblyospora* and *I. pseudoreducta*, none of the named species is particularly closely related to *I. albomarginata* (Fig. 1).

Two undescribed taxa are most similar to *I. albomarginata* in their ITS (SH1144361.09FU, in Fig. 1 represented by KR673688 and LC623536; and SH1144362.09FU, in Fig. 1 represented by KF041394). The two Asian sequences form the sister clade to *I. albomarginata*, which is phylogenetically well supported (98/100/1) in Fig. 1. The described species most similar in the ITS, but with less than 90% similarity rather distant, are *I. flavoalbida* Matheny & Bougher and *I. praecox* Kropp, Matheny & Nanagy. *Inocybe flavoalbida* is a small-spored species with entirely pruinose stipe. It differs from *I. albomarginata*, e.g., by the paler pileus colour and habitat, since it was found in mixed subtropical rainforest in Australia and Papua New Guinea (Matheny & Bougher 2017). Neither the ITS of the holotype nor that of the paratypes of *I. praecox* has been published, but the sequences indicated in Fig. 1 as *I. praecox* are identical in their LSU to the holotype of *I. praecox*. *Inocybe praecox* can be distinguished by larger and stouter basidiomata, a partially appressed squamulose pileus surface and clavate to fusiform-ventricose hymenial cystidia. It is a vernal species and was described from western Washington state (USA); the sequences used here for the species stem from across the border, from British Columbia (Canada).

Inocybe amblyospora Kühner, Bull. Soc. Naturalistes Oyonnax 9 (suppl.): 3 (1955) (Figs. 3, 8b)

Description and iconography: Kühner (1955).

Typification

Lectotype designated by Poirier (2016: 54): FRANCE, Savoie, above Avenches, "Pierre Larron" [alt. 1770 m], moist location with *Picea abies*, under *Adenostyles*, 18 Aug. 1937 [leg. R. Kühner] (G00058748).

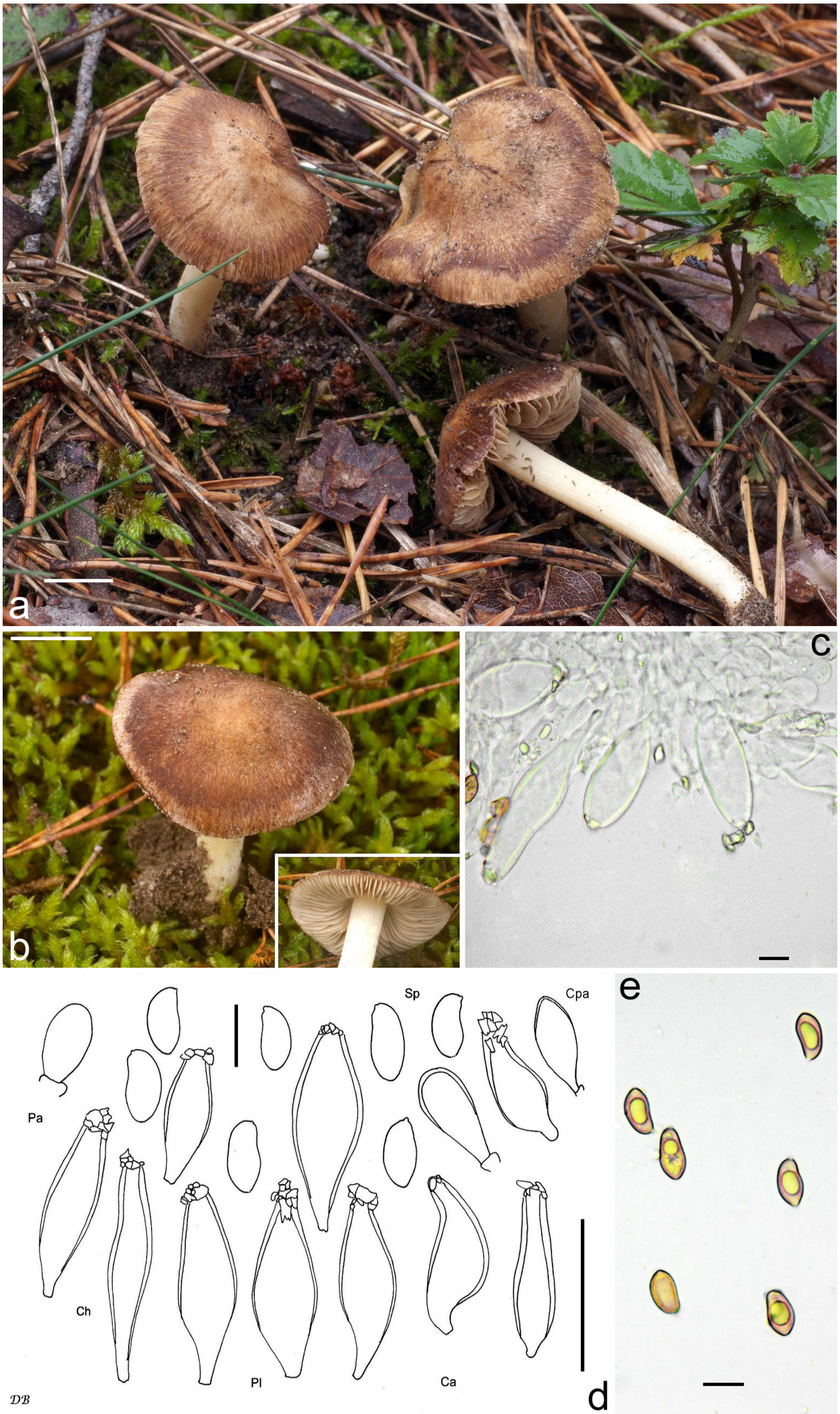

Fig. 6. *Inocybe centesima*. **a**. Holotype, scale bar: 1 cm. **b**. Coll. DB31-10-21-1, scale bar: 1 cm. **c**. Cheilocystidia (DB25-10-17-2), scale bar: 10 µm. **d**. Microscopic characters (holotype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e**. Spores (holotype), scale bar: 10 µm.

Description

Pileus 20–40 mm wide, at first (sub)conical to subcampanulate, later conico-convex, convex or expanded, with or without a more or less pronounced large umbo, margin at first involute or decurved, later decurved to straight or even uplifted and then pileus depressed around the centre; when young, with faint remnants of a greyish velipellis, visible sometimes also later at the centre of the pileus; colour dark brown with reddish hue to dark reddish brown (Mu 5YR 4/3–4/6, 3/3–3/4; 7.5YR 3/4), sometimes up to blackish brown at the centre; surface at first smooth and shiny glabrous, later still shiny and smooth or slightly verrucose at the centre, outwards minutely appressed floccose or rim(ul)ose to minutely innately fibrillose; young basidiomata with remnants of a cortina. *Lamellae* from moderately crowded to subdistant (c. 40–50, l = 1–3), broadly adnate, subventricose, at first whitish to whitish-greyish, later pale yellowish to pale ochraceous-brownish; edge strongly fimbriate, whitish. *Stipe* 30–60 × 3–7 mm, rather stout, cylindrical or widening towards the base, base thickened to (sub)bulbous, at first entirely covered by fine whitish tomentum, later longitudinally striate to glabrous, at first very pale brownish, then brownish to intensely red-brown, near the base and at the extreme apex remaining whitish and thus sometimes with strong colour contrast; rather roughly pruinose over its entire length. *Context* whitish in pileus and stipe, brownish in the cortex of the stipe when old. *Smell* indistinct. *Colour of exsiccata*. Pileus brown to dark brown with reddish hue (Mu YR 7/5YR 4/4–4/6, 3/4), lamellae a little lighter in colour, stipe concolorous or a little darker in colour, no darkening or blackening on drying.

Spores 7.2–10.0 µm (av. 8.4 µm, SD 0.4 µm) × 3.9–5.0 µm (av. 4.4 µm, SD 0.2 µm); Q = 1.6–2.3 (av. 1.9, SD 0.1) (n = 120 of 3 coll.), smooth, mostly narrow (sub)ellipsoid or subcylindrical, with or without a suprahilar depression, apex obtuse, rarely subobtuse. *Basidia* 25–30 × 7–9 µm, generally 4-spored, rarely also 2-spored and then spores up to 10 µm. *Pleurocystidia* 39–74 µm (av. 58 µm, SD 8 µm) × 12–23 µm (av. 17 µm, SD 3 µm), Q = 1.7–5.6, av. 3.6, SD 0.9) (n = 45 of 3 coll.), mostly (sub)utriform, also (sub)fusiform or subcylindrical, with sometimes a rather long neck, usually with a short, but sometimes with a long pedicel, apex usually with only small crystals, walls up to 1.0 (1.5) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size, intermixed with numerous colourless (sub)clavate, (sub)cylindrical or subglobose, thin-walled paracystidia. *Pileipellis* constituted of an epicutis made up of parallel hyphae 5–12 µm wide, with encrusting and parietal brownish to brown pigment, subcutis with wider and paler to colourless elements, intermixed with thin-walled colourless cauloparacystidia. *Caulocystidia* on the entire length of the stipe, 35–60 × 10–15 (20) µm, broadly (sub)fusiform, (sub)utriform, rarely (sub)clavate, apex usually crystalliferous, walls up to 1.0 µm thick at the apex, pale yellowish-greenish with 3% KOH, intermixed with colourless (sub)-clavate, thin-walled cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe amblyospora was found by us with *Picea abies* at high montane to subalpine altitudes, often in rather moist conditions. One collection was found on a small island in the middle of a brook, another on a moist slope crisscrossed by springlets. This fits very well to what Kühner wrote about the location of the holotype (see below). Besides our own collections from Austria and Germany, no other sequences of basidiomata or EcM or soil-samples are known to us. Thus, the species seems to be rather rare.

Type specimens examined

Lectotype (G00058748). *Spores* 7.3–10.0 µm (av. 8.8 µm, SD 0.7 µm) × 3.6–4.8 µm (av. 4.4 µm, SD 0.3 µm); Q = 1.7–2.4 (av. 2.0, SD 0.2) (n = 40), smooth, oblong, mostly (sub)cylindrical, apex obtuse. *Basidia* 4-spored. *Pleurocystidia* 52–75 µm (av. 62 µm, SD 8.0 µm) × 8–19 µm (av. 14 µm, SD 3.1 µm); Q = 3.1–6.5 (av. 4.7, SD 1.0) (n = 15), (sub)cylindrical, (sub)fusiform or subutriform, apex usually crystalliferous, walls up to 1.0 (1.5) µm thick, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size. *Paracystidia* not observed. *Caulocystidia* not studied (stipe was not sent by the herbarium).

Additional specimens examined

AUSTRIA, Tirol, Imst, Silz, Kühtai, ÖK25V 2221-Ost, alt. 1780 m, *Picea abies,* 20 Aug. 2012, leg. D. Bandini & B. Oertel (DB20-8-12-12). Salzburg, Tamsweg, Prebersee, ÖK25V 3230-Ost, alt. 1500 m, moist location with *Picea abies*, *Alnus* sp., 10 Aug. 2013, leg. D. Bandini (SMNS-STU-F-0901742, DB10-8-13-11). Salzburg, Zederhaus, Riedingtal, ÖK25V 3229-Ost, alt. 1490 m, moist location with *Picea abies*, 18 Sep. 2020, leg. D. Bandini (DB18-9-20-25). GERMANY, Bayern, Ostallgäu, Pfronten, Breitenberg, TK25 8429/3, alt. c. 1800 m, very moist location with *Alnus viridis*, *Picea abies*, 19 Aug. 2012, leg. D. Bandini & B. Oertel (DB19-8-12-15). Bayern, Ostallgäu, Halblech, Ammergebirge, TK25 8431/1/3, alt. 1400 m, *Picea abies*, 17 Sep. 2018, leg. D. Bandini (SMNS-STU-F-0901741, DB17-9-18-9).

Notes

Inocybe amblyospora is characterized by a dark brown to dark reddish brown pileus colour, smooth to rim(ul)ose or minutely fibrillose pileus surface, faint greyish velipellis, stipe pruinose over entire length, smooth, on average short and narrow spores, mostly (sub)utriform hymenial cystidia often with a rather long neck, and broadly (sub)fusiform or (sub)utriform caulocystidia. It can be found at montane to subalpine altitudes with conifers. The species has been mistaken for *I. albomarginata* (see under *I. albomarginata*), which differs from *I. amblyospora*, e.g., by lacking a velipellis, by the often areolate-diffracted or somewhat cracked pileus centre, flat lamellae and shorter spores, as

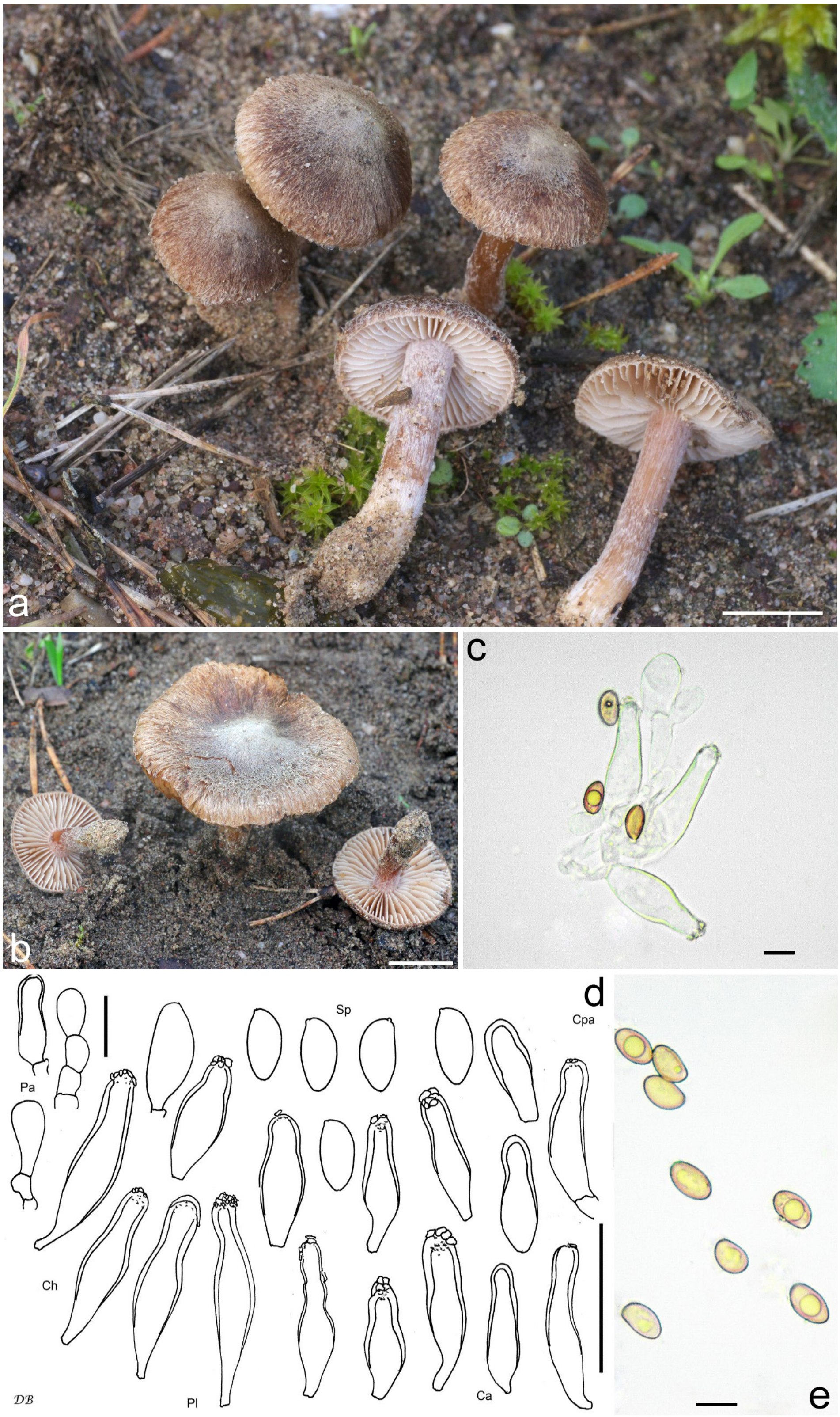

Fig. 7. *Inocybe rufuloides*. **a**. Epitype, scale bar: 1 cm. **b**. Coll. DB31-10-21-4, scale bar: 1 cm. **c**. Cheilocystidia and Paracystidia (epitype), scale bar: 10 µm. **d**. Microscopic characters (epitype); Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm. **e**. Spores (epitype), scale bar: 10 µm.

well as a habitat usually at lower altitudes (see above). *Inocybe bonii* has, e.g., on average shorter but wider spores, on average smaller hymenial cystidia and longer, mostly narrow utriform or subcylindrical caulocystidia with mostly a long and undate neck. The spores and hymenial cystidia of *I. suecica* are on average wider, and the species grows with frondose trees (Vauras & Larsson 2016; DB, personal observation). *Inocybe brijunica* Mešić, Tkalčec & Haelew. can be distinguished from *I. amblyospora*, e.g., by stipe pruinose only near the apex or at least not in the lower half, much shorter spores and shorter hymenial cystidia, as well as a Mediterranean habitat (Mešić et al. 2021), and *I. demetris*, e.g., by the abundant velipellis, on average wider spores, hymenial cystidia often with undate walls, and much longer caulocystidia (Bandini et al. 2022b). *Inocybe pseudoreducta* differs, e.g., by pileus surface more decidedly rimose with age, spores often shaped like apple-seeds with (sub)conical apex, as well as habitat usually at lower altitudes (Stangl & Glowinski 1981; La Rosa et al. 2017).

The two available sequences for *I. amblyospora* received high ufb and pp support (100and 1, respectively) in Fig. 1. The species is clearly distinct from all other described or unnamed taxa. *Inocybe amblyospora* is, with around 90% similarity in the ITS, only very distantly related to *I. praecox*, which has larger basidiomata than *I. amblyospora*, a paler pileus colour, on average wider spores, clavate to ventricose fusiform hymenial cystidia, and occurs in spring (Kropp et al. 2010 and see above under *I. albomarginata*). We were not allowed to sequence the lectotype of *I. amblyospora*, but since the macroscopic and microscopic details of our own collections match well with those of the type, and since the habitat is the same, we are confident that the collections we sequenced are *I. amblyospora* and consider our sequences suitable as surrogates for a type sequence, at least until data from the type become available.

Inocybe bonii Bandini, Valade & U. Eberh., **sp. n.**
(Fig. 4; MycoBank: MB 849355)

Etymology

Named "bonii" in honour of Marcel Bon, who was an outstanding inocybologist.

Diagnosis

Inocybe bonii has a brown pileus colour, mostly with reddish hue, at most rimose pileus surface, entirely pruinose stipe, smooth spores, size on average 8.3 × 5.0 µm, mostly (sub)fusiform hymenial cystidia, pleurocystidia measuring on average 52 × 13 µm, and narrow utriform or subcylindrical caulocystidia with mostly a long and undate neck. It grows on calcareous soil. It can be recognized by the combination of the above characteristics and differs in its ITS sequence from other species, such as *I. albomarginata* or *I. pseudoreducta*.

Holotype

GERMANY, Baden-Württemberg, Alb-Donau-Kreis, Merklingen, Widderstall, TK25 7424/3, alt. 850 m, *Picea abies*, *Fagus sylvatica*, 30 Sep. 2021, leg. D. Bandini (STU SMNS-STU-F-0901743; isotype priv. herb. D.B. DB30-9-21-3).

Description

Pileus 10–30 mm wide, at first (sub)conical to subcampanulate, later broadly convex or expanded, often without, otherwise with a more or less pronounced large umbo, margin at first decurved, later straight to even uplifted and then depressed around the centre; young basidiomata with remnants of a pale greyish velipellis visible even later at the centre but vanishing when moist; colour brown in different shades, mostly with reddish hue (Mu 10YR 5/4–5/6, 4/4–4/6; 7.5YR 4/4–4/6; 5YR 4/4–4/6), with age sometimes strongly paling, either towards the margin or entirely; surface at first smooth and glabrous, with age either remaining glabrous or getting from minutely rimulose to strongly rimose towards the margin, with diverging fibres so that the paler context below is visible; no remnants of a cortina observed. *Lamellae* moderately crowded (c. 35–60, l = 1–3), adnate, sometimes with subdecurrent tooth, subventricose, long time whitish, later greyish-whitish and with age greyish-brownish with a more or less intense ochraceous hue; edge often irregular, even, whitish. *Stipe* 30–70 × 2–5 mm, straight or curved, base even to thickened or even submarginate bulbous, when young entirely covered with thin whitish tomentum, later longitudinally striate to glabrous, at first whitish, then flesh-coloured to pale reddish or even rather intense reddish-brownish, base/bulb whitish; pruinose on entire length, though sparsely in the lower half. *Context* whitish in the pileus, faintly brownish or reddish-brownish in the cortex of the stipe, whitish in the base/bulb. *Smell* (sub)spermatic, at least when cut. *Colour of exsiccata*. Pileus brown to dark reddish brown (Mu 5YR 4/3–4/6, 3/2–3/4; 7.5YR 4/4–4/6), lamellae and stipe concolorous, no darkening or blackening on drying.

Spores 7.3–9.2 µm (av. 8.3 µm, SD 0.4 µm) × 4.5–5.6 µm (av. 5.0 µm, SD 0.2 µm); Q = 1.4–2.0 (av. 1.6, SD 0.1) (n = 120 of 3 coll.), smooth, (sub)amygdaloid, mostly without a suprahilar depression, apex (sub)acute, with indistinct pseudoporus. *Basidia* 21–28 × 7–10 µm, generally 4-spored, rarely also 2-spored and then spores up to 10.5 µm. *Pleurocystidia* 41–65 µm (av. 52 µm, SD 6 µm) × 9–18 µm (av. 13 µm, SD 2 µm); Q = 2.8–6.7 (av. 4.2, SD 0.9) (n = 45 of 3 coll.), mostly (sub)fusiform, sometimes also (sub)utriform or sublageniform, usually without or with only short neck but occasionally also with a longer neck, walls sometimes somewhat undate, mostly with a rather short pedicel, apex usually crystalliferous, walls up to 2.5 (3.0) µm thick at the apex, yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size, intermixed with numerous colourless, (sub)clavate, thin-walled paracystidia. *Pileipellis* constituted of an epicutis

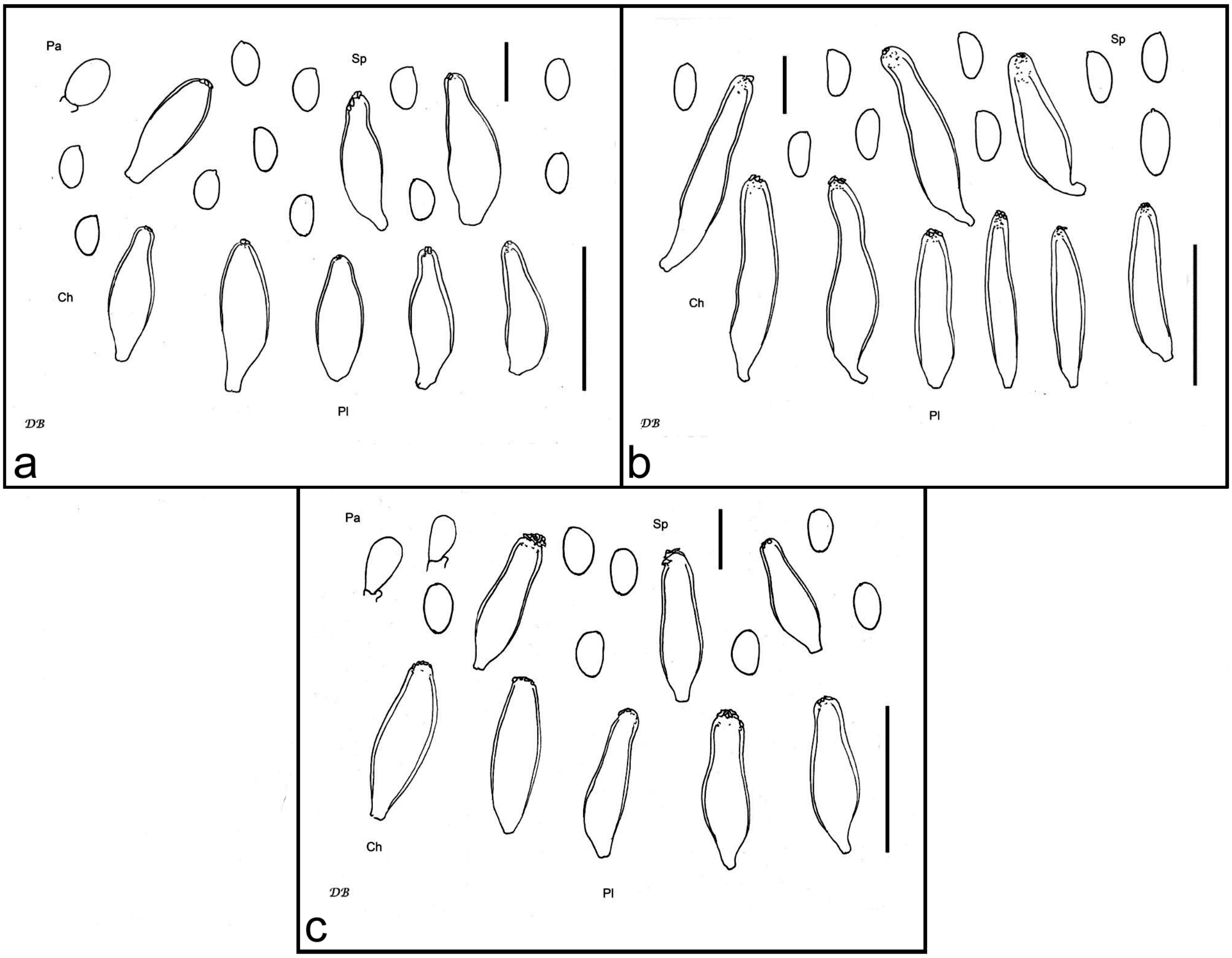

Fig. 8. Microscopic characters of type collections. **a**. *Inocybe albomarginata* (PRC-bottle n°119). **b**. *I. amblyospora* (G00058748). **c**. *I. reducta* (C-F-67157). Ca = Caulocystidia, Cpa = Cauloparacystidia, Ch = Cheilocystidia, Pa = Paracystidia, Pl = Pleurocystidia, Sp = Spores; scale bar spores: 10 µm, scale bar cystidia: 50 µm.

made up of parallel hyphae 4–11 µm wide, with encrusting and parietal brown to dark brown pigment, subcutis with wider and paler to colourless elements, up to 15 µm wide. *Caulocystidia* on entire length of the stipe, but only sparsely in the lower half, 50–95 × 8–13 µm, narrow utriform or subcylindrical, mostly with a long neck with undate walls, with a short pedicel or sometimes with truncate base, apex usually crystalliferous, walls up to 1.5 µm thick at the apex, yellowish-greenish with 3% KOH, intermixed with (sub)clavate to (sub)cylindrical, thin-walled cauloparacystidia. *Clamp-connections* abundant in all tissues.

Habitat and distribution

Inocybe bonii was found by us on calcareous soil with conifers or frondose trees, in France and Germany. In GenBank and UNITE (SH0570962.09FU, 2.0% = SH0017908.09FU, 3%) there are no other sequences from basidiomata, but EcM sequences from Germany (HF675192), Switzerland (MN970792), and soil-samples from Estonia, Greece, Iran, Israel, Italy and Morocco that might also represent *I. bonii*.

Additional specimens examined

FRANCE, Charente-Maritime, Lozay, bois d'Essouverts, 46.028158 N, -0.537226 W, alt. 88 m, *Pseudotsuga menziesii*, *Picea abies*, 20 Nov. 2019, leg. F. Valade (DB20-11-19-Valade, FV2019112002). GERMANY, Sachsen-Anhalt, Börde, Weferlingen, TK25 3632/3, *Quercus robur*, *Carpinus betulus*, 14 Oct. 2013, leg. E. Preikschas (SMNS-STU-F-0901747, DB14-10-13-Preikschas). Bayern, Ostallgäu, Füssen, cemetery, TK25 8430/1, alt. 800 m, *Picea abies*, 22 Sep. 2021, leg. D. Bandini (SMNS-STU-F-0901744, DB22-9-21-8). Baden-Württemberg, Alb-Donau-Kreis, Merklingen, Widderstall, TK25 7424/3, alt. 850 m, *Picea abies*, *Fagus sylvatica*, 30 Sep. 2021, leg. D. Bandini (SMNS-STU-F-0901745, DB30-9-21-5).

Notes

Inocybe bonii is characterized by an often reddish-hued brown, smooth to rimose pileus surface, pale greyish velipellis, when aging an up to intensely reddish-brownish stipe pruinose on its entire length but only sparsely so in the lower half, on average rather small smooth spores and mostly (sub)fusiform hymenial cystidia as well as narrow utriform or subcylindrical caulocystidia with a mostly long and undate neck. The species can be mistaken for several other species with small spores such as *I. albomarginata*, which differs, e.g., by lacking a velipellis, by the often areolate-diffracted or somewhat cracked pileus centre, flat, long time whitish lamellae and smaller spores (see above). *Inocybe amblyospora* differs, e.g., by the usually darker pileus colour, when aging less rimose pileus surface, the reduced and very fugacious velipellis, and narrower, oblong, often (sub)cylindrical spores with (sub)obtuse apex as well as habitat usually in higher montane areas (see above), and *I. brijunica*, e.g., by the usually darker brown pileus colour without reddish tinges, smaller spores and Mediterranean habitat (Mešić et al. 2021). *Inocybe comis* Bandini & B. Oertel has a finely tomentose to minutely or strongly lanose pileus, stipe pruinose only near the apex, spores mostly with an explicit suprahilar depression and caulocystidia often with subcapitate apex (Bandini et al. 2022b), whereas *I. demetris* usually has fewer reddish tinges and never reddish pilei, mostly (sub)utriform to (sub)lageniform hymenial cystidia sometimes with undate neck, on average longer spores and longer hymenial cystidia (Bandini et al. 2022b). *Inocybe glabripes* Ricken differs from *I. bonii* by usually lacking reddish tinges in the pileus colour, at most a finely rimose pileus surface, stipe pruinose only near the apex, smaller spores and shorter hymenial cystidia (see, e.g., Ricken 1910–1915; Lange 1917, as "*I. microspora*"; Kuyper 1986; Stangl 1989; Bandini et al. 2021c), *I. minimispora*, e.g., by the only faint reddish hue in the pileus colour, fugacious whitish velipellis, stipe pruinose only near the apex, smaller spores and shorter caulocystidia (Reumaux 1986; Bandini et al. 2021c), and *I. heterosemen*, e.g., by the at the centre reddish and towards the margin yellow-ochraceous pileus colour, on average smaller spores and shorter, often (sub)clavate hymenial cystidia (Carteret & Reumaux 2012; Bandini et al. 2022b). *Inocybe pseudoreducta* has on average shorter, mostly ovoid or apple-seed shaped spores and plumper, on average wider hymenial cystidia and mostly (sub)fusiform, often somewhat deformed caulocystidia not with an undate neck, whereas *I. suecica* never has an almost reddish pileus colour, pileus often much darker at the centre than towards the margin, stipe not becoming intensely reddish-brownish with age but paler, and hymenial cystidia often with a clearly demarcated transition from the bulge to the neck, and usually growing on more rich and less dry terrain (Vauras & Larsson 2016; DB, personal observation). The pileus of *I. virgatula* Kühner has at most a faint reddish hue, the stipe is pruinose only near the apex, has larger spores with a suprahilar depression and on average larger hymenial cystidia (Kühner 1955; Stangl 1974; Bandini et al. 2021c).

Based on available data, it is not clear whether soil sequences included in the same sh as sequences that quite clearly represent *I. bonii* all represent the species or whether *I. bonii* has a very close unnamed sister taxon. The distribution data could suggest that *I. bonii* s. str. has a temperate distribution and some of the sequenced soil samples a more Mediterranean one, but this is based on a very small number of samples and could be misleading. We here decided to treat *I. bonii* in the narrower sense. Phylogenetically, based on ITS and LSU, the closest relative is *I. demetris* (see Fig. 1); in terms of ITS similarity, *I. comis* and *I. glabripes* rank almost the same as *I. demetris* (all around 93%).

Inocybe carolina Bandini, Rodr.-Campo & U. Eberh., **sp. n.**

(Fig. 5; MycoBank: MB 849356)

Etymology

Named "carolina" ("belonging to Carolus", i.e., Carl) after Carl von Linné.

Diagnosis

Inocybe carolina has a brown to dark brown pileus colour, long time smooth and glabrous, with age only minutely innately fibrillose pileus surface, abundant whitish velipellis, stipe pruinose only near the apex, smooth spores measuring on average 9.2 × 5.6 µm, a usually rather plump and rather thin-walled, variously shaped hymenial cystidia, and pleurocystidia measuring on average 68 × 14 µm. It grows on dry calcareous soil and is probably associated with *Pinus*. It can be recognized by the combination of the above characteristics and differs in its ITS sequence from other species, such as *I. venerabilis* or *I. rufobrunnea*.

Holotype

SPAIN, Comunidad de Madrid, Guadalix de la Sierra, 40.774700 / -3.640960, alt. 827 m, in an abandoned limestone quarry, at mossy location close to *Pinus sylvestris*, *Populus nigra* and *Juniperus oxycedrus*, 26 Nov. 2018, leg. A. Díaz-Fernández, J.A. Rodea-Butragueño, M. García-Aranda & F.J. Rodríguez-Campo (holotype MA-Fungi 98710; isotypes priv. herb. F.J. Rodríguez Campo PRC-181126-05, STU SMNS-STU-F-0901789, priv. herb. D.B. DB26-11-18-Rodr.-Campo).

Description

Pileus 5–35 mm wide, at first subconical to subcampanulate or subglobose, later broadly convex or expanded, usually without an umbo, margin at first decurved, later straight or even uplifted when old, and then pileus depressed around the umbo; young basidiomata thickly covered by a layer of whitish velipellis, visible also later at least at the centre of the pileus; colour brownish to dark brown (Mu 10YR 4/3–4/6, 3/4–3/6; 7.5 YR 3/4), but mostly somewhat speckled because of remnants of the velipellis; surface at first and often long time smooth and glabrous, later sometimes minutely innately fibrillose with fine fibres; young basidiomata with faint remnants of a whitish cortina. *Lamellae* moderately crowded (c. 35–50, l = 1–3), broadly adnate with a (sub)decurrent tooth, even to (sub)ventricose, at first whitish, later creamy to greyish-whitish, with age greyish-brownish; edge strongly fimbriate, whitish. *Stipe* 20–40 × 2–7 mm, often rather stout, straight to curved, sometimes widening towards the base or base widened or even bulbous, when young covered with whitish tomentum, later longitudinally striate to glabrous, at first pale flesh-coloured, later ochraceous brownish, with or without reddish tinge, and pale to sometimes rather intensely reddish near the apex; roughly pruinose only near the apex of the stipe. *Context* watery whitish in the pileus and at first also in the stipe, later greyish-whitish to reddish brown, at least in the cortex of the upper half of the stipe. *Smell* indistinct or subspermatic to slightly disagreeable. *Colour of exsiccata*. Pileus dark brown (Mu 7/5YR 3–4; 10YR 3/3–3/6), lamellae and stipe concolorous or a little lighter in colour, no darkening or blackening on drying.

Spores 8.0–10.6 µm (av. 9.2 µm, SD 0.6 µm) × 4.8–6.8 µm (av. 5.6 µm, SD 0.4 µm); Q = 1.4–2.0 (av. 1.7, SD 0.1) (n = 160 of 4 coll.), smooth, often rather heterogeneous in size, mostly broadly (sub)amygdaloid, usually without and only rarely with a faint suprahilar depression, apex mostly (sub)acute. *Basidia* 24–42 × 8–13 µm, generally 4-spored, rarely also 2-spored. *Pleurocystidia* 45–91 µm (av. 68 µm, SD 8 µm) × 10–19 µm (av. 14 µm, SD 2 µm); Q = 3.1–7.2 (av. 4.9, SD 1.0) (n = 60 of 4 coll.), rather plump (sub)utriform, (sub)cylindrical, subfusiform or (sub)clavate, without or with only a short neck, often with more or less undate walls, sometimes with a rounded and occasionally cap-like thickened apex, with a short pedicel or with truncate base, apex crystalliferous or not, walls up to 1.0 (1.5) µm thick at the apex, but mostly rather thin-walled, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in size but somewhat more variable in shape, intermixed with numerous colourless, (sub)clavate, thin-walled, sometimes catenate paracystidia. *Pileipellis* constituted of an epicutis made up of parallel hyphae 4–12 µm wide, with encrusting and parietal dark brown pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only near the apex of the stipe, 35–70 × 10–15 µm, often rather plump (sub)fusiform, (sub)cylindrical to (sub)clavate, apex with or without small crystals, walls up to 1.0 µm thick at the apex, pale yellowish-greenish with 3% KOH; intermixed with some colourless, (sub)clavate, thin-walled cauloparacystidia. *Clamp-connections* abundant in all tissues.

Habitat and distribution

Inocybe carolina was found by us in Austria and Spain, always on dry calcareous soil. In Austria it was found on the gravelly border of a small road, not far from the river Lech, in the vicinity of *Helianthemum*, *Dryas* and various species of gentians and orchids. The collections from Spain were found in an abandoned limestone quarry. This calcareous area is a small hill located next to the Pedrezuela reservoir, with *Quercus ilex* as the predominant tree species and various other species at the foot of the quarry: *Populus nigra*, *Juniperus oxycedrus* and *Pinus sylvestris*. Species hypothesis SH1235752.09FU, 1.5% presumably represents *I. carolina*, with a specimen sequence from Italy (JF908222) and soil sample sequences from Morocco. Probably not all sequences in the corresponding species hypothesis at 3% (SH0200216.09FU) represent *I. carolina*.

Additional specimens examined

AUSTRIA, Tirol, Reutte, Rieden, ÖK25V 2215-West, alt. 790 m, *Pinus sylvestris*, *Juniperus* sp., 8 Sep. 2019, leg. D. Bandini (DB8-9-19-22). Tirol, Reutte, Weißenbach am Lech, at the wayside, ÖK25V 2215-West, alt. 870 m, *Pinus sylvestris*, 9 Oct. 2021, leg. D. Bandini (DB9-10-21-7). SPAIN, Comunidad de Madrid, Guadalix de la Sierra, 40.77769 / -3.64081, alt. 830 m, in an abandoned limestone quarry, mossy location near *Pinus sylvestris*, *Populus nigra* and *Juniperus oxycedrus*, 16 Nov. 2015, leg. J. A. Rodea-Butragueño & A. Díaz-Fernández (MA-Fungi 98709, priv. herb. PRC-151116-02, SMNS-STU-F-0901790, DB16-11-15-Rodr.-Campo). Ibidem, 23 Oct. 2020, leg. J.A. Rodea-Butragueño & F. J. Rodríguez-Campo (MA-Fungi 98711, priv. herb. PRC-201023-01, DB23-10-20-Rodr.-Campo). Ibidem, 27 Oct. 2021, leg. J.A. Rodea-Butragueño, A. Díaz-Fernández & F.J. Rodríguez-Campo (MA-Fungi 98712, priv. herb. PRC-211027-01, DB27-10-21-Rodr.-Campo).

Notes

Inocybe carolina is characterized by the brown to dark brown pileus colour, long time smooth and glabrous, with age only minutely innately fibrillose pileus surface, abundant whitish velipellis, stipe pruinose only near the apex, smooth broadly (sub)amygdaloid spores and usually rather plump and rather thin-walled, differently-shaped hymenial cystidia, as well as rather plump (sub)fusiform to (sub)clavate caulocystidia. The habitat was for all our collections dry calcareous soil with *Pinus* nearby. In Austria, *I. venerabilis* Bandini, B. Oertel & U. Eberh. was found in the same habitat. This species differs from *I. carolina*, e.g., by the smaller basidiomata, greyish velipellis, larger spores and often shorter hymenial cystidia (Bandini et al. 2022b). *Inocybe aurantiobrunnea* Esteve-Rav. & García Blanco, a species described from Spain, differs, e.g., by the less abundant velipellis, orange to orange-yellow lamellae and larger spores (Esteve-Raventós et al.

2003; Bandini et al. 2022a), while *I. costinitii* Bizio, Ferisin & Dovana, also a Mediterranean species, has larger spores, often subcylindrical thicker-walled hymenial cystidia and usually long and narrow (sub)cylindrical to (sub)fusiform caulocystidia (Bizio et al. 2016; Bandini et al. 2021c). *Inocybe rufobrunnea* J. Favre can be distinguished from *I. carolina*, e.g., by the more fragile basidiomata, less smooth pileus surface, greyish velipellis and much larger spores (Favre 1955; Kuyper 1986, as "*I. rufuloides* var. *exilis*"; Bandini et al. 2022b), *I. tarda* Kühner, e.g., by the sometimes almost blackish brown pileus colour, less abundant and darker velipellis, larger spores and longer, often somewhat deformed caulocystidia often with undate walls (Kühner 1955; Bandini et al. 2021c, 2022a), *I. filiana*, e.g., by the usually smaller and more fragile basidiomata, with age often less smooth pileus surface, less abundant velipellis and shorter and not plump hymenial cystidia (Bandini et al. 2022b). Furthermore, it can be found on more acidic soil. *Inocybe aerea* E. Ludw. has more fragile basidiomata, a less smooth pileus surface, fugacious and less abundant greyish velipellis and narrower spores, and it grows near *Salix* (Ludwig 2017; DB, personal observation), whereas, *I. furfurea* Kühner differs from *I. carolina*, e.g., by the usually paler pileus colour, with age scabby, cracked and/or fissured pileus centre, fugacious and less abundant greyish velipellis and on average much shorter spores (e.g., Kühner 1955; Kuyper 1986; Stangl 1989; Bandini et al. 2019c). *Inocybe griseovelata* Kühner usually has a paler pileus colour, more greyish velipellis, longer spores and very long and narrow caulocystidia (Kühner 1955; Kuyper 1986; Stangl 1989; Bandini et al. 2021c, 2022a), and *I. grusiana* Bandini & B. Oertel can be distinguished from *I. carolina*, e.g., by the greyish velipellis, longer spores and long and narrow, subcylindrical caulocystidia (Bandini et al. 2021c).

Inocybe aurantiobrunnea is the most similar described species to *I. carolina*, with a 94% sequence identity in the ITS. As for *I. bonii*, without morphology it is difficult to delimit *I. carolina* clearly against EcM and soil data, although in this case the support for *I. carolina* s. str. is, with 89/100/1, better than for the clades including soil or EcM sequences. In Fig. 1, *I. carolina* is interpreted in the strict sense.

Inocybe centesima Bandini, G. Bandini & U. Eberh., **sp. n.**

(Fig. 6; MycoBank: MB 849357)

Etymology

Named "centesima" because it is the hundredth new species described by D. Bandini and co-authors.

Diagnosis

Inocybe centesima has an at the centre pale brownish, outwards dark brown pileus colour with a purple hue, smooth to at most rim(ul)ose pileus surface, entirely pruinose stipe, smooth, mostly almost kidney-shaped spores measuring on average 11.6 × 6.0 µm, mostly (sub)fusiform hymenial cystidia, pleurocystidia measuring on average 55 × 19 µm, and growing on sandy calcareous soil with *Pinus sylvestris*. It can be recognized by the above combination of characteristics and differs in its ITS sequence from other species, such as *I. psammobrunnea* or *I. rufobrunnea*, that can be found in the same habitat.

Holotype

GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, near Nature Reserve Düne Pferdstrieb, TK25 6617/4, alt. 113 m, *Pinus sylvestris*, 25 Oct. 2017, leg. D. Bandini (STU SMNS-STU-F-0901749; isotype priv. herb. D.B. DB25-10-17-2).

Description

Pileus 20–35 mm wide, at first (sub)conical, later broadly convex or expanded, with or without low, large umbo, margin slightly decurved, later straight or even uplifted, and then pileus depressed around the umbo; young basidiomata with faint and fugacious remnants of a pale greyish velipellis; usually somewhat bicoloured, pale ochraceous brownish to pale nut-brown at the centre and sometimes with age also at the margin, outside the centre brown with a more or less intense purplish hue (Mu 10YR 5/6–5/8; 5YR 5/6–5/8; 10R 3/4–3/6); surface at first smooth and glabrous, later finely rim(ul)ose towards the margin; no remnants of a cortina observed. *Lamellae* moderately crowded (c. 40–60, l = 1–3), irregular, adnate, (sub)ventricose, at first whitish then dingy whitish with greyish hue or greyish to greyish-brownish; edge fimbriate, whitish. *Stipe* 40–60 × 3–5 mm, cylindrical or widening towards the base, base always thickly covered with sand, equal or slightly thickened; at first covered with fine whitish tomentum, later longitudinally striate or glabrous, at first whitish, later dingy whitish to ivory or beige; pruinose on entire length. *Context* dingy or watery whitish in the pileus, whitish in the stipe. *Smell* spermatic, at least when cut. *Colour of exsiccata*. Pileus dark brown with reddish hue (Mu 5YR 3/3–3/4; 7.5YR 3/4), lamellae a little lighter and stipe much paler in colour, no darkening or blackening on drying.

Spores 10.0–13.6 µm (av. 11.6 µm, SD 0.8 µm) × 5.3–7.1 µm (av. 6.0 µm, SD 0.3 µm); Q = 1.7–2.3 (av. 1.9, SD 0.1) (n = 120 of 3 coll.), smooth, mostly very characteristically almost kidney-shaped, with a suprahilar depression, apex subacute to subobtuse, with small indistinct pseudoporus. *Basidia* 25–30 × 7–11 µm, generally 4-spored, but also 2-spored. *Pleurocystidia* 37–73 µm (av. 55 µm, SD 8 µm) × 14–24 µm (av. 19 µm, SD 2 µm); Q = 1.9–4.9 (av. 2.9, SD 0.6) (n = 45 of 3 coll.), usually ventricose (sub)fusiform, at the apex generally wide, without or with only a short neck, usually without or with a short pedicel, apex usually crystalliferous, walls up to 1.5 (2.0) µm thick at the apex, pale yellowish-greenish with 3% KOH. *Cheilocystidia* similar in appearance and size, intermixed with numerous colourless, (sub)clavate or subcylindrical, thin-walled paracystidia. *Pileipellis* constituted of an epicutis made up of parallel hyphae 4–12 µm wide, with encrusting and parietal brownish to dark brown pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* on the entire length of the stipe, but only sparsely in the lower half due to abrasion through sand particles, 30–55 × 10–18 µm, mostly (sub)lageniform or (sub)fusiform, apex usually crystalliferous, without or with only a short neck and pedicel, walls up to 1.5 µm thick at the apex, pale yellowish-greenish with 3% KOH; intermixed with numerous (sub)clavate to subglobose cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe centesima was found by us on calcareous sandy terrain (inland dunes) with *Pinus sylvestris* in Germany. No other collections or sequences in databases are known to us.

Additional specimens examined

GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, Nature Reserve Galgenbuckel, TK25 6617/4, alt. 112 m, *Pinus sylvestris*, *Helianthemum nummularium*, 31 Oct. 2021, leg. D. & G. Bandini (SMNS-STU-F-0901750, DB31-10-21-1). Baden-Württemberg, Rhein-Neckar-Kreis, Walldorf, TK25 6617/4, alt. 120 m, *Pinus sylvestris*, 6 Nov. 2021, leg. D. & G. Bandini (SMNS-STU-F-0901787, DB6-11-21-2). Baden-Württemberg, Rhein-Neckar-Kreis, St. Ilgen, TK25 6617/4, alt. 115 m, *Pinus sylvestris*, 14 Nov. 2021, leg. D. & G. Bandini (SMNS-STU-F-0901751, DB14-11-21-1).

Notes

Inocybe centesima is characterized by an at the centre pale brownish, outwards dark brown pileus colour with purple hue, smooth to at most rim(ul)ose pileus surface, only faint and fugacious pale greyish velipellis, an entirely pruinose stipe, rather large, smooth, mostly almost kidney-shaped spores and mostly (sub)fusiform hymenial cystidia. The shape of the spores of *I. centesima* is very unusual and the contrasting pileus colour of older basidiomata with purple tinges is quite extraordinary as well. Two species can be found at the same location: *I. psammobrunnea* Bon, differing from *I. centesima*, e.g., by the often large greyish patch at the centre of the pileus, with age up to intensely reddish-pinkish stipe, and shorter (sub)amygdaloid and not almost kidney-shaped spores (Bon 1990; Poirier 2002, as "*I. griseotarda*"; Bandini et al. 2021c), and *I. tarda*, also growing in the same location and which can be distinguished from *I. centesima* by, e.g., stipe with age often entirely reddish of different intensities, on average shorter (sub)amygdaloid and not almost kidney-shaped spores, on average longer hymenial cystidia and longer caulocystidia (Kühner 1955; Bandini et al. 2021c, 2022a). *Inocybe tjallingiorum* Kuyper usually has a darker centre of the pileus, no purple tinges in the pileus colour, stipe with age intense brown to red-brown or even darker, and much smaller, (sub)amygdaloid to (sub)ellipsoid spores (Kuyper 1986; Stangl 1989; Bandini et al. 2021c), whereas *I. serotina* has a larger, paler patch of velipellis at the pileus centre, larger, mostly (sub)amygdaloid and not almost kidney-shaped spores and mostly (sub)clavate or subglobose hymenial cystidia. Furthermore, *I. serotina* is usually found on sea-shores (Peck 1904; Lange 1940; Kuyper 1986; DB, personal observation). The Mediterranean species *I. neorufula* Esteve-Rav., Macau & Ferville differs from *I. centesima*, e.g., by the whitish velipellis, more reddish-tinged, much smaller, not almost kidney-shaped spores and on average longer hymenial cystidia (Esteve-Raventós et al. 2012; DB, personal observation), and *I. rufuloides*, e.g., by the lack of purple tinges in the pileus colour, less smooth pileus surface, (sub)amygdaloid or almost elliptic, not almost kidney-shaped spores and often subcapitate on average shorter hymenial cystidia (see below). *Inocybe metrodii* can be distinguished, e.g., by the darker centre of pileus and lack of purple tinges in the pileus colour, much smaller, not almost kidney-shaped spores, and habitat not on inland dunes but on richer soil (Stangl & Veselský 1979; Bandini et al. 2021c), *I. phaeoleuca* Kühner, e.g., by the lack of purple tinges in the pileus colour and the smaller and (sub)amygdaloid, not almost kidney-shaped spores (Kühner 1955; Kuyper 1986, as "*I. splendens* var. *phaeoleuca*"; Bandini et al. 2019c), and *I. splendens* R. Heim, e.g., by the shorter navicular and not almost kidney-shaped spores and on average longer hymenial cystidia, as well as growth with frondose trees (Heim 1931; Kuyper 1986, as "*I. splendens* var. *splendens*"; Bandini et al. 2019c).

The species clade of *I. centesima* is well supported (94/99/1). We are not aware of any ITS sequences more similar to *I. centesima*. No species genetically closely related to *I. centesima* are known as yet, and the sequences forming the sister clade of *I. centesima* are at most 95% similar. With only 86% identity in the ITS, *I. pararubens* Carteret & Reumaux is the most closely, yet quite distantly related described species. It differs from *I. centesima*, e.g., by the darker centre of pileus and lack of purple tinges in the pileus colour, smaller, (sub)amygdaloid to (sub)navicular spores and growth with frondose trees (Carteret & Reumaux 2012; DB, personal observation). *Inocybe centesima* is by all indications a rare species.

Inocybe rufuloides Bon, Doc. Mycol.14(no. 53): 28 (1984) (Fig. 7)

Selected description and iconography: Bon (1984, 1990); Kuyper (1986); Lantieri (2005); Bougher & Matheny (2011).

Typification

Holotype: FRANCE, Somme, Cayeux-sur-Mer, Brighton-La Mollière, *Pinus*, 18 May 1983, leg. M. Bon, J. Vast & G. Claus, (LIP-MB83038).

Epitype (designated here; MBT 10014038): GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Walldorf, TK25 6617/4, alt. 120 m, *Pinus sylvestris*, 6 Nov. 2021, leg. D. & G. Bandini (STU SMNS-STU-F-0901753; dupl. priv. herb. D.B. DB6-11-21-4).

Description

Pileus 10–40 mm wide, at first (sub)conical, later broadly convex or expanded, with or without a large umbo, margin at first slightly inflexed, soon deflexed, later straight or even uplifted when old and then depressed around the umbo; young basidiomata entirely covered by a greyish velipellis, still visible at the umbo of older basidiomata; colour brown to dark brown, often with reddish hue in different nuances (Mu 10YR 4/3–4/6, 3/4–3/6; 5YR 4/3–4/6; 7.5YR 4/4–4/6), but when young often greyish-brownish because of the velipellis; surface at first sometimes almost smooth, but usually finely tomentose to minutely lanose, with age coarsely lanose, sometimes somewhat lacerate; young basidiomata with faint remnants of a cortina. *Lamellae* rather distant (c. 25–35 (40), l = 1–3), thickish, narrowly to broadly adnate, (sub)ventricose, at first whitish, later greyish-brownish to brown with reddish hue; edge uneven fimbriate, whitish. *Stipe* 15–45 × 2–5 mm, stout, straight or curved, base often somewhat thickened, at first entirely covered with whitish tomentum, later longitudinally striate or glabrous, reddish brown at different intensities to intensely red-brown, base mostly remaining whitish; pruinose with sparse, rough pruina only near the apex of the stipe. *Context* whitish in the pileus, red-brown in the upper half of the stipe. *Smell* spermatic, at least when cut. *Colour of exsiccata*. Pileus pale brown, greyish-brownish (Mu 10YR 5/4–5/6, 4/2–4/6), lamellae and stipe concolorous or a little lighter in colour, no darkening or blackening on drying.

Spores 9.7–13.4 µm (av. 11.4 µm, SD 0.8 µm) × 5.5–7.1 µm (av. 6.4 µm, SD 0.3 µm); Q = 1.4–2.1 (av. 1.8, SD 0.1) (n = 120 of 3 coll.), smooth, oblong (sub)amygdaloid or almost elliptic, with or without a faint suprahilar depression, apex subacute to subobtuse, with indistinct pseudoporus. *Basidia* 25–32 × 9–12 µm, generally 4-spored, rarely also 2-spored. *Pleurocystidia* 34–69 µm (av. 48 µm, SD 7.3 µm) × 10–20 µm (av. 14 µm, SD 2.1 µm); Q = 2.3–4.8 (av. 3.4, SD 0.6) (n = 45 of 3 coll.), variously shaped, often subcapitate, (sub)cylindrical, (sub)utriform, (sub)fusiform, (sub)lageniform), sometimes even (sub)clavate, at the apex generally wide, mostly with only a short neck, with a short pedicel or with truncate base, apex usually crystalliferous, walls up to 1.5 (2.0) µm thick at the apex, often abruptly thickened at the neck, yellow-green with 3% KOH. *Cheilocystidia* similar in appearance and size, intermixed with numerous colourless to sometimes somewhat brownish, (sub)clavate, (sub)cylindrical or subglobose or somewhat deformed, thin- to slightly thick-walled, sometimes catenate paracystidia. *Pileipellis* constituted of an epicutis made up of parallel hyphae 4–12 µm wide, with encrusting and parietal brownish pigment, subcutis with wider and paler to colourless elements. *Caulocystidia* only near the apex of the stipe, 30–60 × 10–15 µm, (sub)utriform, (sub)cylindrical or even (sub)clavate, but mostly somewhat deformed and often with undate walls, without or with only a short neck, without or with a short pedicel or with truncate base, apex crystalliferous or not, walls up to 1.0 (1.5) µm thick at the apex, yellow-green with 3% KOH; intermixed with numerous, mostly but sometimes somewhat brownish, (sub)clavate to subglobose, thin-walled colourless cauloparacystidia. *Clamp connections* abundant in all tissues.

Habitat and distribution

Inocybe rufuloides was found by us only in the calcareous sand of inland dunes or adjacent areas, always with *Pinus sylvestris* nearby. However, only *Quercus* was recorded for the collection from Algeria. The taxon appears to correspond to SH0146902.09FU, 3%, which includes specimen sequences from Algeria, Australia, Italy, Germany and Spain, an EcM sequence from France and soil sample sequences from Italy and Morocco. Based on this, the species appears to be widely distributed and not rare. Bougher & Matheny (2011) considered *I. rufuloides* as an introduced taxon in Australia.

Additional specimens e„xamined

ALGERIA, Bainem, *Quercus ilex*, 31 Dec. 2014, leg. S. Aouali (DB31-12-14-Aouali). GERMANY, Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, Nature Reserve "Düne Pferdstrieb", TK25 6617/4, alt. 100 m, *Pinus sylvestris*, *Quercus robur*, *Helianthemum*, 13 Oct. 2012, leg. D. Bandini, B. Oertel & W. Winterhoff (SMNS-STU-F-0901442, DB13-10-12-4). Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, TK25 6617/4, alt. 113 m, *Pinus sylvestris*, *Helianthemum*, *Quercus robur*, 21 Oct. 2012, leg. D. Bandini & B. Oertel (DB21-10-12-14). Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, Nature Reserve "Düne Pferdstrieb", TK25 6617/4, alt. 113 m, *Pinus sylvestris*, 23 Oct. 2021, leg. D. & G. Bandini (DB23-10-21-2). Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, Nature Reserve "Galgenbuckel", TK25 6617/4, alt. 112 m, *Pinus sylvestris*, *Helianthemum nummularium*, 31 Oct. 2021, leg. D. & G. Bandini (SMNS-STU-F-0901752, DB31-10-21-5). Baden-Württemberg, Rhein-Neckar-Kreis, Sandhausen, Nature Reserve "Galgenbuckel", TK 6617/4, alt. 112 m, *Pinus sylvestris*, *Helianthemum nummularium*, 6 Nov. 2021, leg. D. & G. Bandini (DB6-11-21-4). Baden-Württemberg, Rhein-Neckar-Kreis, Walldorf, TK25 6617/4, alt. 120 m, *Pinus sylvestris*, 6 Nov. 2021, leg. D. & G. Bandini (DB6-11-21-5).

Notes

A description of the holotype was given in Bandini et al. (2020c). We have tried and failed to generate PCR products from this collection; others appear to have failed, too. According to our experience, it is only rarely possible to successfully sequence material collected by M. Bon. We decided to choose an epitype for the species as the type material did not display all morphological details necessary for its delimitation, for instance the caulocystidia at the top of the stipe and the paracystidia of young basidiomes. In the protologue, Bon (1984) described the latter as abundant and sometimes catenate. A plate of the microscopic details and measurements of the spores and pleurocystidia of the type were published in Bandini et al. (2020c).

Inocybe rufuloides is characterized by a usually rather stout habit, brown to dark brown pileus colour with more or less intense reddish hue, with age mostly lanose pileus surface, abundant pale greyish velipellis, stipe with age up to intensely red-brown, pruinose only near the apex, rather large spores, and often subcapitate hymenial cystidia with many, sometimes catenate and slightly thick-walled paracystidia. *Inocybe carneicaulis* E. Ludw. differs, e.g., by the smoother pileus surface, usually quite uniformly (sub)-fusiform, usually not (sub)capitate hymenial cystidia and not catenate or slightly thick-walled paracystidia (Ludwig 2017; DB, personal observation), *I. coriacea*, e.g., by the smaller and less stout basidiomata, usually paler pileus colour, on average smaller spores and usually not subcapitate hymenial cystidia (Bandini et al. 2022c), and *I. deianae* Eyssart., e.g., by the velipellis usually not remaining at the centre of the pileus of older basidiomata, on average shorter spores and usually not subcapitate hymenial cystidia (Eyssartier 2007; Brugaletta et al. 2019, as "*I. lapidicola*"; Bandini et al. 2022a). *Inocybe distantifolia* E. Ludw. can be distinguished from *I. rufuloides*, e.g., by the smaller pileus, smoother pileus surface, on average smaller spores and usually not subcapitate hymenial cystidia (Ludwig 2017), and *I. laurina* Bandini, B. Oertel & C. Hahn, a species found by us next to *I. rufuloides*, can be distinguished from the latter, e.g., by the whitish velipellis, smoother pileus surface, smaller spores and longer, usually not subcapitate hymenial cystidia (Bandini et al. 2020a). *Inocybe psammobrunnea* has a smoother pileus surface, smaller spores and on average longer and usually not subcapitate hymenial cystidia (Bon 1990; Poirier 2002 (as "*I. griseotarda*"); Bandini et al. 2021c), *I. neorufula* has a whitish velipellis, smoother pileus surface and smaller spores (Esteve-Raventós et al. 2012; DB, pers. obs.) and *I. rufobrunnea* has a smoother pileus surface, larger spores and usually not subcapitate hymenial cystidia (Favre 1955; Kuyper 1986, as "*I. rufuloides* var. *exilis*"; Bandini et al. 2022b). *Inocybe tarda* differs from *I. rufuloides*, e.g., by having less velipellis, a smoother pileus surface, on average shorter spores and on average longer, usually not subcapitate hymenial cystidia (Kühner 1955; Bandini et al. 2021c, 2022a).

Inocybe rufuloides is well supported (97/100/1) and well delimited in Fig. 1, in a clade including a number of unnamed sequences. Among the described and sequenced species, *I. filiana* is most similar in the ITS to *I. rufuloides* (87%). This species differs from *I. rufuloides*, e.g., by the usually smaller and more fragile basidiomata, usually smoother pileus surface, smaller spores and not often subcapitate hymenial cystidia (Bandini et al. 2022b).

Discussion

The species described in depth above, *I. albomarginata*, *I. amblyospora*, *I. bonii*, *I. carolina*, *I. centesima* and *I. rufuloides*, are well delimited and distinguishable from all other known species morphologically and molecularly. However, for narrowing down the species limits of *I. bonii* (and to a lesser extend *I. carolina*), further studies will be necessary to find out whether sister clades of environmental sequences of *I. bonii* and *I. carolina* s. str. are artefactual or not. These studies would include the analysis of additional loci and study of basidiomata that are phylogenetically (ITS) representatives of the sequences that are neither clearly belonging to nor clearly distinct from clades with sequences from material with known morphology. We have kept the inclusion of soil sequences at a minimum, because it is often not clear whether the variation found within these sequences is due to sequence variants not obvious in Sanger sequences or to sequence errors. The included environmental sequences were used to show how clear or not the molecular identification and delimitation of the new taxon was.

All six species named above belong to clades that have also been retrieved in earlier studies (Bandini et al. 2020c, 2021c, 2022a, 2022b), but leaving out many clades in between. Fig. 1 supports earlier results that morphological characters used for identification are a poor predictor for phylogenetic results: While three species with small spores and entirely pruinose stipes, *I. albomarginata*, *I. amblyospora* and *I. pseudoreducta*, are all in the same supported clade (Fig. 1, part 2), *I. bonii*, with the same characters, is not. *Inocybe centesima* (Fig. 1, part 1) is phylogenetically supported as a member of the *I. splendens* clade in a wider sense, including species with and without trademark Splendentes characters. The supported clade depicted in Fig. 1, part 4, starting from *I. cincinnata* down to *I. carolina*, contradicts in part supported results in Bandini et al. (2021c, 2022b); subclades, however, were consistent (taking into account that the sets of included species were different). In terms of consistent results, *I. carolina* is probably best considered as a member of the *flocculosa* clade.

The three new species described above were from calcareous habitats, and two of them, *I. carolina* and *I. cen-*

tesima, seem to associate, possibly even exclusively, with *Pinus*. Furthermore, they were found on inland dunes, a very special habitat that is at times very dry and hot, in open terrain in an old limestone quarry, and in sun-lit gravelly ground on the side of a road. Only a few weeks per year, if at all, inocybes can be found there.

Inocybe carolina and *I. centesima* also have in common that they are very constant in their characteristics, since both the macroscopic aspect and the microscopic details in all collections of both species are very consistent. This is rather rare among the Inocybaceae, since generally either the macroscopic or the microscopic characters, or both, vary, sometimes significantly, as can be observed within the third new species, *I. bonii*, where the macroscopic aspect can be quite different from collection to collection (see Fig. 4a, b). The habitat of *I. bonii* is not as extreme as that of the other two species, but it is also very dry at times and strictly calcareous. *Inocybe bonii* has quite small spores and an entirely, though in the lower half often rather sparsely, pruinose stipe. Therefore, and because the macroscopic aspect is quite variable, this species can be mistaken for several other species with small spores and an entirely pruinose stipe or stipe pruinose only near the apex, as for instance *I. albomarginata*, *I. pseudoreducta* and *I. suecica*, or even *I. virgatula*, which macroscopically may look like the type collection of *I. bonii*. Because *I. albomarginata* and *I. amblyospora* are sometimes confused with each other or with other species (see above), we decided to give portraits of both species and select an epitype for *I. albomarginata*, the lectotype of which, being preserved in formaldehyde together with several fruitbodies belonging to other genera, is in very bad condition.

According to the key of Bon (1997a), *I. centesima* would belong to the Section *Splendentes* R. Heim ex Singer, which groups species with an entirely pruinose stipe. Demonstrating a problem associated with Bon's classification, *Inocybe bonii* could be included either in the section *Splendentes* or in the section *Tardae* because of the stipe only sparsely pruinose in the lower half. *Inocybe carolina* belongs to the section *Tardae* (Bon 1997a).

Inoybe carolina has been found more often in Spain than in central Europe and forms a clade phylogenetically embedded among other species (*I. aurantiobrunnea*) or clades representing Unite sh with proponents from areas with hot summers. For *I. carolina*, it is tempting to assume a southerly origin, or at least a strictly Mediterranean distribution after the last glacial period, and a temperature-driven northward expansion. Větrovský et al. (2019), in their meta-study of fungal distribution patterns, posited that temperature is one of the main drivers of species distribution. With increasing temperatures, one might expect an increasing number of species like *I. tigrina* (Bandini et al. 2021c) with a large distribution area covering both Southern and Central Europe and potentially even Northern Europe. However, if Větrovský et al. (2019) was correct about the narrower climatic tolerances of ectomycorrhizal fungi in comparison to other fungi, distribution areas might shift northwards rather than extend.

Species with updated typification

Inocybe geophylla (Bull.) P. Kumm., Führer Pilzk.: 78 (1871)

Basionym: *Agaricus geophyllus* Bull., Herb. France 11: pl. 522, fig. 2 (1791).

Typification

Lectotype, designated here (MBT 10003226): Bulliard (1791), Herbier de la France 11: pl. 522, fig. 2 (*Agaricus geophyllus*).

Epitype, selected in Bandini et al. (2021c: 1058): AUSTRIA, Tirol, Reutte, Höfen, ÖK25V 2215-West, alt. 970 m, *Picea abies*, 23 Sep. 2015, leg. D. Bandini (STU SMNS-STU-F-0901531; dupl. priv. herb. D.B. DB23-9-15-31).

Notes

This species was discussed in detail and epitypified in Bandini et al. (2021c). The here designated lectotype was cited as the holotype in the latter publication. As mentioned in the introduction, epitypes only serve as interpretative types for the material that is cited in the epitypification and not for syntypes. For purposes of epitypification, illustrations are better considered lectotypes, because illustrations cannot represent the entire type that ever existed. Furthermore, the designation of an illustration as lectotype, rather than citing it merely as holotype, protects the epitypification against other illustrations, variations of the same illustration, etc. that might exist and could be considered syntypes based on the original description. Lectotypification in cases such as this (even if no competing syntype is known at the time) avoids potential ambiguity and ensures nomenclatural stability. With this in mind, we decided to follow up the earlier epitypification with a lectotypification.

Inocybe griseovelata Kühner, Bull. Soc. Naturalistes. Oyonnax 9(Suppl. (Mém. hors sér. 1)): 4 (1955)

Typification

Lectotype, designated here (MBT 10014039): FRANCE, Paris, Bois de Vincennes, in a circle of more than 20 fruiting bodies on soil, with frondose trees, near the lake, 8 Jun.1930, leg. R. Kühner (G00058738)

Notes

The collection date of this collection agrees with the protologue. This lectotypification supersedes the lectotypification of Bandini et al. (2021c) [Art. 9.12 (Turland et al.

2018)], who selected a collection with a (presumed) earlier collection date because the above collection seemed to have been lost, when ordered by us in 2018. In the above publication, we cited a wrong G accession number for the earlier collection; the correct number for that specimen is G00566267. The collection G00058738, from June 8th 1930, was suggested earlier as lectotype by J. Poirier (herbarium note, 16 Jan. 1995), but this was, to the best of our knowledge, never formally published. With the correction of the lectotypification, also the epitype SMNS-STU-F-0901568 designated in Bandini et al. (2022a) loses its standing (Art. 9.20. Note 8). We have not had the opportunity to study the lectotype G00058738. Therefore, it would be premature to assign an epitype. The species was discussed in detail in Bandini et al. (2021c, 2022a).

Inocybe hirtella Bres., Fungi Trident. 1(4–5): 52 (1884)

Typification

Lectotype, designated here (MBT 10006582): ITALY, northern Italy. Bresadola (1884) Fungi Trident., 1(4-5): plate 58, fig. 1.

Epitype, selected in Bandini et al. (2022b: 118): GERMANY, Niedersachsen, Emsland, Haselünne, TK25 3310/4, alt. 20 m, *Corylus avellana*, *Quercus robur*, *Pinus sylvestris*, 4 Oct. 2020, D. Bandini (STU SMNS-STU-F-0901607; dupl. priv. herb. D.B. DB4-10-20-19).

Notes

The species was discussed in detail in Bandini et al. (2022b). The selected illustration was cited as holotype there. See under *I. geophylla* for an explanation of the lectotypification.

Inocybe tarda Kühner, Bull. Soc. Naturalistes Oyonnax 9 (Suppl. (Mém. hors sér. 1)): 6 (1955)

Typification

Lectotype, designated by Poirier (2016: 55): FRANCE, Paris, Bois de Vincennes, *Pinus*, 22. Nov. 1933, leg. R. Kühner (G00058745).

Epitype, selected in Bandini et al. (2022a: 55): GERMANY, Rheinland-Pfalz, Rhein-Pfalz-Kreis, near Dudenhofen, TK25 6616/3, alt. 105 m, sandy soil with *Quercus robur*, *Corylus avellana*, *Pinus sylvestris*, 3 Oct. 2017, leg. D. Bandini (STU SMNS-STU-F-0901730; dupl. priv. herb. D.B. DB3-10-17-6).

Notes

The species was discussed in detail and epitypified in Bandini et al. (2022a). The lectotype was cited as holotype in the latter publication. Kühner (1955) did not cite collection numbers. Other material from the same place and date might exist that would have to be considered as syntype had the lectotypification not been done by Poirier (2016). Epitypes only serve as interpretative types for the material that is cited in the epitypification and not for syntypes. Thus, the typification of *I. tarda* is settled and less ambiguous than one might conclude from Bandini et al. (2022a).

Inocybe tigrina R. Heim, Encyclop. Mycol., 1 Le Genre Inocybe (Paris): 230 (1931)

Typification

Lectotype, designated here (MBT 10015420): FRANCE, near Meaux, *Pinus*, Oct. 1929, leg. Mauguin. Heim (1931) Le Genre Inocybe, Plate XIX, fig. 6.

Epitype, designated in Bandini et al. (2021c: 1099): GERMANY, Rheinland-Pfalz, Bad Kreuznach, Lützelsoon, near Kellenbach, alt. 400 m, *Picea abies*, *Fagus sylvatica*, *Pseudotsuga menziesii*, 24 Oct. 2015, leg. D. Bandini & B. Oertel (STU SMNS-STU-F-0901532; dupl. priv. herb. D.B. DB24-10-15-3).

Notes

The species was discussed in detail in Bandini et al. (2021c). The here-designated lectotype was listed as holotype there. See under *I. geophylla* for an explanation of the lectotypification.

Inocybe transitoria (Britzelm.) Sacc., Syll. fung. 5: 788 (1887)

Basionym: *Agaricus transitorius* Britzelm., Ber. Naturhist. Vereins Augsburg 26: 137 (1881).

Typification

Lectotype, designated here (MBT 10015421): GERMANY, Bayern, Krumbach. Britzelmayr (1881), Ber. Naturhist. Vereins Augsburg 26: Abb. 11.

Epitype, selected in Bandini et al. (2022a: 58): NORWAY, Telemark, Kragerø, Kammerfossåsen, *Tilia*, *Fraxinus*, *Populus* forest on clay ground, margin of meadow, under *Tilia* and *Populus*, 15 Jul. 2016, leg. T. E. Brandrud TEB-45-16 (O-F-304850).

Notes

The species was discussed in detail in Bandini et al. (2022a). The illustration designated as lectotype here was cited as holotype in the latter publication. A collection by J. Stangl deposited in M (M-0022272) and referred to by Stangl & Kuyper (1985) and Stangl (1989) is labelled as neotype but was apparently never published as type, neither (incorrectly) as neotype nor as epitype. See under *I. geophylla* for an explanation of the lectotypification.

Funding

This study was financed by the authors and the 'Gesellschaft zur Förderung des Naturkundemuseums Stuttgart'. Other than the authors, the funders had no influence on the research and this manuscript.

Acknowledgements

We are grateful to curators Christian Lange (C), Régis Courtecuisse (LIP) and Ondřej Koukol (PRC) for information and the loan of types in their keeping and are grateful to Holger Thüs (SMNS) for handling the numerous loans for us. We are indebted to Michèle Gendre and Juan Carlos Zamora (G), e.g., for pointing out missing lectotypifications to us. Justice Babic-

Trammell is thanked for her support of the molecular work in Stuttgart. We again greatly appreciate the help of Shaun R. Pennycook and Volker Braun with all kinds of questions around types and nomenclature.

Molecular analyses (sequencing) were carried out within the framework of the Mycoseq project of the Mycological Society of France (SMF, Paris) and the Centre for Functional and Evolutionary Ecology (CEFE, Montpellier), and at Staatliches Museum für Naturkunde Stuttgart. The 'Gesellschaft zur Förderung des Naturkundemuseums Stuttgart' is thanked for their financial support.

We would furthermore like to express our gratitude to Souhila Aouali, Antonio Díaz-Fernández, Eckhard Preikschas and José Antonio Rodea-Butragueño for providing us with fresh collections or specimens or for other help.

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Manuscript received: 08.VII.2023; accepted: 28.X.2023.

Appendix 1. Sequences used in this study. Herbarium abbreviations follow Index Herbariorum (http://sweetgum.nybg.org/science/ih/), with the exception of D.B. = private herbarium of Ditte Bandini. Accession numbers in bold print were obtained in the context of this study. EcM – ectomycorrhizae.

Species/sample	Herbarium	Voucher no.	Other voucher numbers	Origin	GenBank/ UNITE acc. no. ITS	Genbank acc. no. LSU	Published in
Inocybe alberichiana	STU	SMNS-STU-F-0901514	DB12-9-19-16	Austria	MW845855	MW845855	Bandini et al. (2021c)
I. albomarginata	STU	SMNS-STU-F-0901739 (epitype)	DB3-10-19-14	Netherlands	**OR102476**	**OR102476**	
I. albomarginata	STU	SMNS-STU-F-0901740	DB11-9-17-13	Austria	**OR102477**	**OR102477**	
I. albomarginata	DB	DB8-10-20-13		Netherlands	**UDB0799560**		
I. albomarginata as *I. amblyospora*	DB	DB12-7-13-1		Germany	MH366616.2		Bandini et al. (2019b)
I. albomarginata as *I. amblyospora*		UCBSB 93		Pakistan	HG796968		Ilyas, S. et al., submitted 06 Nov. 2013
I. albomarginata as *I. amblyospora*	MCVE	MCVE 21670		Italy	JF908261		Osmundson et al. (2013)
I. albomarginata as *I. amblyospora*	GB	BJ900831		Sweden	AM882908.2		Ryberg et al. (2008)
I. alluvionis as *I. splendens*	GB	EL313-12		France	KJ399959	KJ399959	Larsson et al. (2014)
I. amblyospora	STU	SMNS-STU-F-0901741 (epitype)	DB17-9-18-9	Austria	**OR102479**	**OR102479**	
I. amblyospora	STU	SMNS-STU-F-0901742	DB10-8-13-11	Austria	**OR102480**		
I. angulatosquamulosa	M	M-0281791	JS1408	Germany	MG012474		Bandini et al. (2019b)
I. astraiana	STU	SMNS-STU-F-0901240 (holotype)	DB26-10-14-7	Germany	MN512321	MN512321	Bandini et al. (2020a)
I. athenana	STU	SMNS-STU-F-0901238 (holotype)	DB15-6-19-2	Germany	MN512320	MN512320	Bandini et al. (2020a)
I. aurantiobrunnea	STU	SMNS-STU-F-0001816 (isotype)		Spain	OP164016	OP164016	Bandini et al. (2022a)
I. aurantiobrunnea as *I. luteipes*	MCVE	MCVE 21519		Italy	JF908212		Osmundson et al. (2013)
I. beatifica	STU	SMNS-STU-F-0901261 (holotype)	DB12-10-13-3	Germany	MW845857		Bandini et al. (2021c)
I. beatifica	STU	SMNS-STU-F-0901472	DB22-10-13-1	Germany	MW845859	MW845859	Bandini et al. (2021c)
I. bonii	STU	SMNS-STU-F-0901743 (holotype)	DB30-9-21-3	Germany	**OR102473**	**OR102473**	
I. bonii	STU	SMNS-STU-F-0901745	DB30-9-21-5	Germany	**OR102472**	**OR102472**	
I. bonii	STU	SMNS-STU-F-0901744	DB22-9-21-8	Germany	**OR102474**	**OR102474**	
I. bonii	STU	SMNS-STU-F-0901747	DB14-10-13-Preikschas	Germany	**OR102481**	**OR102481**	
I. bonii	DB	DB20-11-19-Valade		France	**OQ546722**		

Species/sample	Herbarium	Voucher no.	Other voucher numbers	Origin	GenBank/ UNITE acc. no. ITS	Genbank acc. no. LSU	Published in
I. brijunica	PUL	PUL-F27673 (isotype)	D. Haelew. F-1610a	Croatia	MN749370	MN749492	Mešić et al. (2021)
I. brijunica	STU	SMNS-STU-F-0901746	DB17-10-12-2-Dondl	Italy	**OR102467**	**OR102467**	
I. carolina	STU	SMNS-STU-F-0901789 (isotype)	MA-Fungi 98710; PRC-181126-05; DB26-11-18-Rodr. Campo	Spain	**OR102482**	**OR102482**	
I. carolina	STU	SMNS-STU-F-0901748	DB9-10-21-7	Austria	OR102475	OR102475	
I. carolina	STU	SMNS-STU-F-0901790	MA-Fungi 98709; PRC-151116-02; DB16-11-15-Rodr.-Campo	Spain	**OR102483**	**OR102483**	
I. carolina	MA	MA-Fungi 98711	PRC-201023-01; DB23-10-20-Rodr. Campo	Spain	**OR102492**	**OR102492**	
I. carolina	MA	MA-Fungi 98712	PRC-211027-01; DB27-10-21-Rodr.-Campo	Spain	**OR102493**	**OR102493**	
I. carolina as *Inocybe* sp.	MCVE	MCVE 21547		Italy	JF908222		Osmundsen et al. (2013)
I. castorina	STU	SMNS-STU-F-0901250 (holotype)	DB21-10-15-2	Germany	MN512319	MN512319	Bandini et al. (2020a)
I. catalaunica	STU	SMNS-STU-F-0901596	DB5-9-14-3	Germany	OK057187	OK057187	Bandini et al. (2022b)
I. centesima	STU	SMNS-STU-F-0901749 (holotype)	DB25-10-17-2	Germany	**OR102468**	**OR102468**	
I. centesima	STU	SMNS-STU-F-0901787	DB6-11-21-2	Germany	**OR102469**	**OR102469**	
I. centesima	STU	SMNS-STU-F-0901750	DB31-10-21-1	Germany	**OR102471**	**OR102471**	
I. centesima	STU	SMNS-STU-F-0901751	DB14-11-21-1	Germany	OR102478	OR102478	
I. cincinnata	STU	SMNS-STU-F-0901571	DB19-9-20-14	Austria	MW845946	MW845946	Bandini et al. (2021c)
I. clandestina	STU	SMNS-STU-F-0901267	DB11-10-17-16	Germany	MW845865	MW845865	Bandini et al. (2021c)
I. comis	STU	SMNS-STU-F-0901599 (holotype)	DB2013-8-13-3	Austria	OK057190	OK057190	Bandini et al. (2022b)
I. coriacea	STU	SMNS-STU-F-0901683 (holotype)	DB31-10-16-5	Germany	ON003439	ON003439	Bandini et al. (2022b)
I. corydalina	STU	SMNS-STU-F-0900974	DB14-10-12-7	Germany	OR102487	OR102487	
I. costinitii	MCVE	MCVE 28974 (holotype)		Croatia	KX686581		Bizio et al. (2016)
I. cuniculina	KR	KR-M-0043257 (holotype)	DB22-9-11-2	Netherlands	MN625273		Bandini et al. (2020a)
I. deianae	STU	SMNS-STU-F-0901538 (isotype)	DB30-10-4-Eys-sartier	France	OK057117		Bandini et al. (2022b)
I. demetris	STU	SMNS-STU-F-0901593 (holotype)	DB27-10-19-6	Germany	OK057184	OK057184	Bandini et al. (2022b)

Species/sample	Herbarium	Voucher no.	Other voucher numbers	Origin	GenBank/ UNITE acc. no. ITS	Genbank acc. no. LSU	Published in
I. demetris	STU	SMNS-STU-F-0901594	DB27-10-19-10	Germany	OK057185	OK057185	Bandini et al. (2022b)
I. demetris	STU	SMNS-STU-F-0901595	DB22-9-20-13	Germany	OK057186	OK057186	Bandini et al. (2022b)
I. filiana	STU	SMNS-STU-F-0901602 (holotype)	DB4-5-16-1	Germany	OK057192	OK057192	Bandini et al. (2022b)
I. flavoalbida	TENN	TENN 067000 (isotype)	PBM3768	Australia	KJ729873	KJ729901	Matheny et al. (2020)
I. flocculosa	STU	SMNS-STU-F-0901628	DB2-10-19-9	Netherlands	OK057165	OK057165	Bandini et al. (2022b)
I. furfurea	G	G 00053152 (lectotype)		France	MG012472		Bandini et al. (2019b)
I. furfurea	STU	SMNS-STU-F-0901592	DB29-5-21-1	Germany	OK057169	OK057169	Bandini et al. (2022b)
I. fuscicothurnata	TENN	TENN 068940	PBM3980	USA	MF487844	KY990485	Matheny & Swenie (2018)
I. glabrescens	STU	SMNS-STU-F-0901570	DB17-10-17-6	Germany	MW845941	MW845941	Bandini et al. (2021c)
I. glabripes	STU	SMNS-STU-F-0900979 (neotype)	DB2-6-13-12	Germany	MW845881	MW845881	Bandini et al. (2021c)
I. glabripes as *I.* cf. *microspora*	TAA	TAA 185187		Estonia	AM882808.2	AM882808	Ryberg et al. (2008)
I. griseovelata	STU	SMNS-STU-F-0901568 (epitype)	DB30-9-12-1	Germany	MW845942	MW845942	Bandini et al. (2021c)
I. grusiana	STU	SMNS-STU-F-0901262 (holotype)	DB21-5-17-1	Germany	MW845884	MW845884	Bandini et al. (2021c)
I. heterosemen	X. Carteret pers. coll.	XC98091209 (isotype)		France	OK057119		Bandini et al. (2022b)
I. hirtella	STU	SMNS-STU-F-0901607 (epitype)	DB4-10-20-19	Germany	OK057200	OK057200	Bandini et al. (2022b)
I. involuta	STU	SMNS-STU-F-0901270	DB13-10-16-19	Austria	MN512329	MN512329	Bandini et al. (2020b)
I. jucunda	STU	SMNS-STU-F-0901246 (holotype)	DB10-10-15-12	Germany	MW578524	MW578524	Bandini et al. (2021a)
I. langei	STU	SMNS-STU-F-0900983	DB31-8-14-7	Germany	OK057205	OK057205	Bandini et al. (2022b)
I. lapidicola	AMB	AMB 18350		Italy	MN449988		Brugaletta et al. (2019)
I. lasseroides	TENN	TENN 066979		Australia	KP171145	KP170924	Matheny et al. (2020)
I. laurina	STU	SMNS-STU-F-0901247 (holotype)	DB23-10-16-6	Germany	MN512325	MN512325	Bandini et al. (2020a)
I. leochroma	KR	KR-M-0042372 (holotype)	DB25-9-15-21	Austria	MH366611.2		Bandini et al. (2019b)
I. lucis	STU	SMNS-STU-F-0901616 (holotype)	DB23-9-16-14	Germany	ON003441	ON003441	Bandini et al. (2022c)
I. luteifolia	TENN	TENN 022958 (isotype)	CUW PBM2642 (LSU)	USA	FJ436331	EU307814	Kropp & Matheny (2010); Matheny et al. (2020)
I. lutescens	PRM	PRM 823229 (neotype)		Germany	MW845894	**OR100635**	Bandini et al. (2021c), here
I. mecoana	PO	PO-F2158 (holotype)	VF221219IS1	Portugal	OM971872	OM971872	Bandini et al. (2022a)
I. melanopus	GB	BJ920904		Sweden	AM882725	AM882725	Ryberg et al. (2008)

Species/sample	Herbarium	Voucher no.	Other voucher numbers	Origin	GenBank/ UNITE acc. no. ITS	Genbank acc. no. LSU	Published in
I. messapica	AMB	AMB 12794 (holotype)		Italy	MT386024	MT476738	Cervini (2021)
I. metrodii	PRM	PRM756354 (holotype)		Germany	MN319692		Bandini et al. (2021c)
I. metrodii as *I. tenebrosa*	GB	EL8204		Sweden	AM882967.2	AM882967.2	Ryberg et al. (2008)
I. minimispora	STU	SMNS-STU-F-0901264	DB12-7-17-9	Austria	MW845934	MW845934	Bandini et al. (2021c)
I. minimispora as *I. glabripes*	GB	EL8103		Sweden	AM882971.2	AM882971.2	Ryberg et al. (2008)
I. neorufula	STU	SMNS-STU-F-0901287 (isotype)	AH40223	Spain	MT101890		Bandini et al. (2020c)
I. neorufula	STU	SMNS-STU-F-0901445	DB30-10-15-2-Dondl	Italy	MT101876	MT101876	Bandini et al. (2020c)
I. nitidiuscula	M	M-0229745 (epitype)		Germany	KM873364		Marchetti et al. (2014)
I. pallidicremea	TENN	TENN 062552 (PBM2744)	WTU PBM2039 (LSU)	USA	KY990553	AY380385	Matheny (2005); Matheny & Swenie (2018)
I. pararubens	X. Carteret pers.coll.	XC2010-17 (isotype)		France	MN954310		Vauras & Larsson (2020)
I. pararubens	STU	SMNS-STU-F-0900986	DB7-10-12-2	Germany	MW845925	MW845925	Bandini et al. (2021c)
I. perchtana	STU	SMNS-STU-F-0901245 (holotype)	DB21-9-16-18	Austria	MN512326	MN512326	Bandini et al. (2020a)
I. phaeoleuca	PC	PC 0705244	Rom78144	France	MG012476		Bandini et al. (2019b)
I. phaeoleuca	GB	EL297-08		Hungary	KJ399958	KJ399958	Larsson et al. (2014)
I. cf. *praecox* as *I. amblyospora*	UBC	UBC-F19511		Canada	HQ604508	HQ604508	Berbee, M.L. et al., submitted 04 Nov. 2010
I. cf. *praecox* as *I.* cf. *glabrescens*	UBC	UBC-F19019		Canada	HQ604511	HQ604511	Berbee, M.L. et al., submitted 04 Nov. 2010
I. cf. *praecox* as *I. flocculosa*	UBC	UBC-F19374		Canada	HQ604506	HQ604506	Berbee, M.L. et al., submitted 04 Nov. 2010
I. cf. *praecox* as *I. phaeoleuca*	UBC	UBC-F19095		Canada	HQ604503	HQ604503	Berbee, M.L. et al., submitted 04 Nov. 2010
I. praefarinacea	TENN	TENN-F-021176 (isotype)		USA	OP162984		Eberhardt et al. (2023)
I. psammobrunnea	LIP	LIP MB89226 (holotype)	M. Bon 89226	France	MW845926		Bandini et al. (2021c)
I. psammobrunnea	KR	KR-M-0038015		Netherlands	MT101889	**OR100607**	Bandini et al. (2020c), here
I. pseudoreducta	M	M-0138786 (holotype)		Germany	KY213955		La Rosa et al. (2017)
I. pseudoreducta	STU	SMNS-STU-F-0900988	DB1-8-14-3	Germany	**OR102486**	**OR102486**	
I. relicina	KR	KR-M-0038104	DB3-9-9-Kamke	Sweden	OP164031	OP164031	Bandini et al. (2022a)

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I. rivierana	STU	SMNS-STU-F-0901249 (holotype)	DB24-7-18-16	Austria	MW845910	MW845910	Bandini et al. (2021c)
I. roseifolia	CSU	CO5576		USA	MH578026	MK421968	Matheny et al. (2020)
I. rufobrunnea	L	L-0053539 (holotype of *I. exilis*)	Kuyper 2657	Netherlands	MZ667616		Bandini et al. (2022b)
I. rufobrunnea	STU	SMNS-STU-F-0901441	DB28-9-15-16	Austria	MT101873	MT101873	Bandini et al. (2020c)
I. rufuloides	STU	SMNS-STU-F-0901753 (epitype)	DB6-11-21-4	Germany	OR102470	OR102470	
I. rufuloides	STU	SMNS-STU-F-0901752	DB31-10-21-5	Germany	**OR102484**	**OR102484**	
I. rufuloides	STU	SMNS-STU-F-0901442	DB13-10-12-4	Germany	MT101878		Bandini et al. (2020c)
I. rufuloides	J. L. Siquier pers. coll.	JLS 4076		Spain	MK748473		Siquier et al. (2019)
I. rufuloides		CM044		Algeria	KP826750		Benazza, M. et al., submitted 19 Feb. 2015
I. rufuloides	PERTH	PERTH 7700598	E8353	Australia	JN035292		Matheny & Bougher (2017)
I. semifulva	WTU	ACAD11651 (isotype)		Canada	HQ222006		Matheny, P.B. & Wolfenbarger, A.D., submitted 03 Sep. 2010
I. semifulva	STU	SMNS-STU-F-0901000	DB28-8-14-4	Germany	MW845916	MW845916	Bandini et al. (2021c)
I. serotina	GB	EL23706		France	FN550910	FN550910	Ryberg et al. (2010)
I. sindonia	STU	SMNS-STU-F-0901627 (epitype)	DB3-11-13-1	Germany	OK057164	OK057164	Bandini et al. (2022b)
I. splendens	STU	SMNS-STU-F-0901793	DB16-10-15-1b	Germany	OR100705	OR100705	
I. subbrunnea	G	G 00126460 (lectotype)	G 388231	France	KJ399934		Larsson et al. (2014)
I. subbrunnea	STU	SMNS-STU-F-0901619	DB15-9-20-12	Austria	**OR102485**	**OR102485**	
I. suecica	GB	EL60-14 (holotype)		Sweden	KX384177		Vauras & Larsson (2016)
I. tarda	STU	SMNS-STU-F-0901730 (epitype)	DB3-10-17-6	Germany	OP164094	OP164094	Bandini et al. (2022a)
I. tigrina	STU	SMNS-STU-F-0901532 (epitype)	DB24-10-15-3	Germany	MW845933	MW845933	Bandini et al. (2021c)
I. tjallingiorum	L	L-0053540 (holotype)	Kuyper 1902	Netherlands	MW845929		Bandini et al. (2021c)
I. tjallingiorum	KR	KR-M-0038274	DB18-8-11-18	Austria	OP164037	OP164037	Bandini et al. (2022a)
I. venerabilis	STU	SMNS-STU-F-0901605 (holotype)	DB25-5-13-2	Germany	OK057198	OK057198	Bandini et al. (2022b)
I. virgatula	G	G 00058741 (lectotype)		France	MW845923		Bandini et al. (2021c)
I. virgatula as *I. fuscidula*	GB	EL9505		Finland	AM882886.2	AM882886.2	Ryberg et al. (2008)
Inocybe sp.	KA	KA13-1218		Korea	KR673688		Kim et al. (2015)

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Inocybe sp. as *I. abjecta*	UBC	UBC-F-19255		Canada	HQ604211	HQ604211	Berbee, M.L. et al., submitted 04 Nov. 2010
Inocybe sp. as *I. ambigua*	TENN	TENN 063866	PAM08082208 (LIP)	France	HQ586855	HQ641096	Matheny, P.B. et al., submitted 10 Nov. 2010
Inocybe sp. as *I. auricoma*	UBC	UBC-F-19651		Canada	HQ604213	HQ604213	Berbee, M.L. et al., submitted 04 Nov. 2010
Inocybe sp. as *I. nitidiuscula*	UBC	UBC F19396		Canada	HQ604206	HQ604206	Berbee, M.L. et al., submitted 04 Nov. 2010
Inocybe sp. as *I. pusio*	UBC	UBC-F19656		Canada	HQ604521	HQ604521	Berbee, M.L. et al., submitted 04 Nov. 2010
Inocybe sp. as *I. subporospora*	MCVE	MCVE 21472		Italy	JF908186		Osmundson et al. (2013)
Nothocybe distincta	CAL, ZT	CAL 1310, ZT 9250 (holotype)		India	KX171343	EU604546	Matheny et al. (2009); Latha et al. (2016)
Pseudosperma spurium	GB	SJ92017 (holotype)		Sweden	AM882784	AM882784	Ryberg et al. (2008)
EcM				Switzerland	MN970792		Rog et al. (2020)
EcM				Italy	GQ469523		Iotti, M. et al., submitted 07 Aug. 2009
EcM				China	LC623536		Qisheng, H. et al., submitted 31 Mar. 2021
Root tip				Mexico	KF041394		Argüelles-Moyao et al. (2017)
Soil				Germany	HF675192		Kapturska, D. et al., submitted 23 Jan. 2013
Soil	TU	TUE000528		Italy	UDB03641138		Tedersoo et al. (2022)
Soil	TU	TUE001309		Morocco	UDB03830313		Tedersoo et al. (2022)
Soil	TU	TUE003033		Croatia	UDB02073561		Tedersoo et al. (2022)
Soil	TU	TUE000519		Italy	UDB03640535		Tedersoo et al. (2022)
Soil	TU	TUE003304		Italy	UDB02138324		Tedersoo et al. (2022)
Soil	TU	TUE000623		Morocco	UDB03650333		Tedersoo et al. (2022)
Soil	TU	TUE000832		Greece	UDB03703857		Tedersoo et al. (2022)
Soil	TU	TUE000832		Greece	UDB03704369		Tedersoo et al. (2022)
Soil	TU	TUE001305		Morocco	UDB03826252		Tedersoo et al. (2022)