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Inocybe vaurasii (Agaricales, Inocybaceae), a new species of the *I. xanthomelas* group and similar European species with asteriform spores

FERNANDO ESTEVE-RAVENTÓS[1,4*], FERMÍN PANCORBO[2,5], ELLEN LARSSON[3,6], YOLANDA TURÉGANO[1,7], GABRIEL MORENO[1, 8] & ALBERTO ALTÉS[1,9]

[1] *Department of Life Sciences (Botany Unit). University of Alcalá, 28805 Alcalá de Henares, Madrid, Spain.*
[2] *Madrid Mycological Society, Real Jardín Botánico. C/ Claudio Moyano 1, 28014 Madrid, Spain.*
[3] *Biological and Environmental Sciences, University of Gothenburg, and Gothenburg Global Biodiversity Centre, Box 461, SE 40530 Göteborg, Sweden*
[4] *fernando.esteve@uah.es; https://orcid.org/0000-0001-8265-5067*
[5] *fpancorbo@gmail.com; https://orcid.org/0000-0002-2397-177X*
[6] *ellen.larsson@bioenv.gu.se; https://orcid.org/0000-0003-4308-4972*
[7] *yolanda.turegano@edu.uah.es; https://orcid.org/0000-0001-6948-2990*
[8] *gabriel.moreno@uah.es; https://orcid.org/0000-0002-9303-7181*
[9] *alberto.altes@uah.es; https://orcid.org/0000-0002-3579-9081*
* *Correspondence author*

Abstract

Inocybe vaurasii is described as a new species belonging to Section *Marginatae* group Xanthomelas. A comparative morphological and molecular study has been carried out with other species showing basidiospores with stellate appearance and similar sizes: *I. xanthomelas*, *I. humilis* and *I. subrimosa*. An ITS bar code was obtained from type materials of all three of these species. The molecular analysis reveals that, despite the similarity in spore-shape, none of the species were closely related, but form distinct clades that are spread out within the Xanthomelas group. SEM photographs of the spores are provided for each of the species studied. A lectotype for *I. subrimosa* is designated and validated and the lectotype previously designated for *I. xanthomelas* is here validated.

Keywords: Agaricomycetes, Basidiomycota, molecular systematics, taxonomy

Introduction

The Xanthomelas group of the genus *Inocybe* (Fr.) Fr. (1863: 346) section *Marginatae* Kühner (1933: 81) includes approximately 30-35 species on the European continent (Esteve-Raventós *et al.*, unpubl.). According to our molecular studies comprising information collected from the international nucleotide sequence databases (GenBank, UNITE database), there are at least half a dozen species yet to be described in Europe. In recent years, new species have been proposed and, in general, it can be said that the members of the Xanthomelas group are well known and interpreted in Europe. Several papers have been published containing extensive references to taxonomic literature including very valuable data, not only descriptive but also molecular, that are helping us to interpret this group (Bandini *et al.* 2019a, 2020, 2021; Cripps *et al.* 2020; Dovana *et al.* 2020; Esteve-Raventós *et al.* 2015, 2016; Franchi *et al.* 2015; Vauras & Larsson 2016). The Xanthomelas group shows a wide diversity in Europe and throughout the Northern Hemisphere. However, based on molecular data, only *Inocybe invadens* Matheny, Bougher & G. M. Gates in Matheny & Bougher (2017: 342) is known with certainty to occur in the Southern Hemisphere (Australia), according to Matheny & Bougher (Matheny & Bougher 2017: 333), who placed it within the Praetervisa/Calospora group.

The Xanthomelas group includes species generally showing small to medium-sized basidiomata and a slender habit, with a dominance of yellow to yellowish-brown colourations in the pileus, originally white or pale yellowish stipe, with a distinct often marginate bulb at the base, no or weak odour and often long cystidia in l/w ratio. With age, most species develop a characteristic and obvious yellowish, yellowish-brown or dark brown pigment in the hyphae; this pigment gives aged or dehydrated basidiomata a dark, brownish, greyish-blackish or even distinctly blackish

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colouration. The pigment is visible in microscopic preparations, often inside the hymenial elements (cystidia and basidia) or in the hyphae of the context, in some species more intensely than in others (Esteve-Raventós *et al.* 2015).

This group of species has often historically been treated either as an integral part of or as a group related to the Praetervisa/Margaritispora group, whose species, although in some cases tend to darken in parts, never acquire such dark colours as they age or dry out. Species of the Praetervisa/Margaritispora group develop a more robust habit, showing a not so evident or not clearly marginate bulb and cystidia with a utriform tendency, and are wide and voluminous (see Esteve-Raventós *et al.* 2016; Larsson *et al.* 2018).

The type species of this group, *I. xanthomelas* Boursier & Kühner (1933: 84), shows a marked blackening of its context, typically asteriform spores and a habitat in deciduous forests, with preference under Fagaceae in limestone soils (Kühner 1933, Esteve-Raventós *et al.* 2015); the present work completes the knowledge of this species with the contribution of the ITS sequences obtained from the lectotype (Esteve-Raventós *et al.* 2015), as well as a paratype of one of Kühner's original samples. The new species here described *I. vaurasii*, shows clear similarities to *I. xanthomelas* with which it has probably been confused in the past.

In addition, further data is presented here for some other species with asteriform spores that also belong to the Xanthomelas group, such as *I. humilis* (J. Favre & E. Horak in Horak 1987: 231) Esteve-Raventós & Vila (1998: 192) and *I. subrimosa* (Karsten 1888: 38) Saccardo (1891: 100), including ITS sequence data generated from type-specimens and additional sequenced collections (Fig. 1, Table 1.). Both, *I. humilis* and *I. subrimosa*, were represented in two of the clades that were presented in the phylogenetic tree of Esteve-Raventós *et al.* (2015) under the names *I. xanthomelas* and *I. sp.* respectively. This contribution aims at clarifying the different interpretations of the name *I. xanthomelas* in the past.

TABLE 1. List of collections used in the molecular analyses along with geographic origin, putative host, vouchers, and GenBank accession numbers. In bold, the sequences generated in this study.

Species	Country	Putative host	Voucher	GenBank accession number		Sequence published in
				ITS	LSU	
Inocybe alpinomarginata	USA	*Salix reticulata/ S. glauca*	CLC1334	MK153646	MK153646	Cripps *et al.* 2020
Inocybe alpinomarginata	Sweden	*Salix herbacea, S. reticulata*	EL207-13 holotype	MK153648	MK153648	Cripps *et al.* 2020
Inocybe antoniniana	**Spain**	***Pinus sylvestris, Fagus sylvatica***	**AH51033**	**ON314579**	**ON314579**	**This study**
Inocybe antoniniana	Turkey	*Fagus sylvatica*	KATO Fungi 4064 holotype	MN988712		Bandini *et al.* 2020
Inocybe blandula	Austria	*Pinus sylvestris*	STU:SMNS-STU-F-0901578	MZ144124	MZ144124	Bandini *et al.* 2021
Inocybe blandula	Austria	*Pinus sylvestris*	STU:SMNS-STU-F-0901577 holotype	MZ144123	MZ144123	Bandini *et al.* 2021
Inocybe caprimulgi	Finland	*Betula, Pinus sylvestris*	JV10514F	KP308782	KP170953	Matheny & Bougher 2017
Inocybe caprimulgi	Finland	*Betula, Pinus sylvestris*	JV5808 holotype	KT958924	KT958924	Vauras & Larsson 2016
Inocybe flavobrunnescens	Spain	*Quercus ilex*	EL440-13	MK153641	MK153641	Cripps *et al.* 2020
Inocybe flavobrunnescens	Portugal	*Quercus faginea*	AH 40466 holotype	KJ938784		Esteve-Raventós *et al*. 2015
Inocybe hirculus	Finland		JV30693	MK153643	MK153643	Cripps *et al.* 2020
Inocybe hirculus	Finland	*Betula pubescens, Picea abies, Pinus sylvestris, Salix sp.*	K51 holotype	FJ531872		Vauras & Kokkonen 2009
Inocybe humilis	**Spain**	***Pinus sylvestris, Betula alba***	**AH 56364**	**ON263577**	**ON263577**	**This study**

...continued on the next page

TABLE 1. (Continued)

Species	Country	Putative host	Voucher	GenBank accession number		Sequence published in
				ITS	LSU	
Inocybe humilis	**Spain**	***Pinus sylvestris, Betula alba***	**AH 45142**	**ON259050**	**ON259050**	**This study**
Inocybe humilis	**Spain**	***Pinus sylvestris, Betula alba, Salix sp.***	**AH 45144**	**ON259051**	**ON259051**	**This study**
Inocybe humilis	**Spain**	***Salix herbacea* cf.**	**AH 23498**	**ON259052**	**ON259052**	**This study**
Inocybe humilis	**Spain**	***Quercus pyrenaica***	**AH 48192**	**ON259053**	**ON259053**	**This study**
Inocybe humilis	**Spain**	***Pinus sylvestris, Betula alba***	**AH 56423**	**ON263163**		**This study**
Inocybe humilis (as *I.* cf. *praetervisa)*	Sweden		EL904	AM882718	AM882718	Ryberg *et. al* 2008
Inocybe humilis (as *I. straminipes)*	France	under *Alnus glutinosa* and *Salix*	PAM01042904 (LIP)	HQ586868	HQ586868	Unpublished
Inocybe humilis (as *I. straminipes)*	United Kingdom	*Betula, Quercus*	HFRG_EJ210709_2 FRDBI 21011309	OL828792		Unpublished
Inocybe humilis (as *I. straminipes*)	France	Alpine, under *Polygonum viviparum*,	PAM95081306 (LIP)	HQ586858	HQ586858	Unpublished
Inocybe humilis (as *I. xanthomelas*)	Spain	*Betula pendula*	AH 29895	KJ938774		Esteve-Raventós *et al.* 2015
Inocybe humilis (as *I. xanthomelas*)	Spain	*Betula pendula, Quercus petrea, Salix atrocinerea*	AH 26954	KJ938773		Esteve-Raventós *et al.* 2015
Inocybe humilis	**Swizterland**	***Picea***	**G00126386 holotype**	**ON227435**		**This study**
Inocybe krieglesteineri	Slovakia	*Quercus pubescens*	EL313-14	KT958914	KT958914	Vauras & Larsson 2016
Inocybe krieglesteineri	Spain	*Pinus radiata*	RFS031213-03 holotype	KJ938768		Esteve-Raventós *et al.* 2015
Inocybe lacunarum	Finland	*Deciduous forest*	JV12244 holotype	KT958908	KT958908	Vauras & Larsson 2016
Inocybe mixtilis	**France**	***Pinus pinaster, Quercus suber***	**AH 51853**	**ON263164**	**ON276737**	**This study**
Inocybe mixtilis	Germany	*Abies*	M 0219661 epitype	KM873369		Marchetti *et al*.2014
Inocybe occulta	**Spain**	***Pinus sylvestris***	**AH 50983**	**ON201510**	**ON201510**	**This study**
Inocybe occulta	Spain	*Quercus ilex subsp. Ballota*	AH 36443 holotype	KX290787		Esteve-Raventós *et al.* 2018
Inocybe phaeocystidiosa	Spain		AH 3953	MK153640	MK153640	Cripps *et al.* 2020
Inocybe phaeocystidiosa	Spain	*Pinus sylvestris*	AH 9154 holotype	KT203789		Esteve-Raventós *et al.* 2016
Inocybe populea	Japan	*Populus nigra*	TAKK1565-5 paratype	KT958911		Vauras & Larsson 2016
Inocybe subrimosa	**Spain**	***Betula alba***	**AH 44475**	**ON259055**	**ON259055**	**This study**
Inocybe subrimosa	**Spain**	***Betula alba***	**AH 09324**	**ON259056**		**This study**
Inocybe subrimosa	**Spain**	***Betula alba***	**AH 44474**	**ON259054**	**ON259054**	**This study**
Inocybe subrimosa (as *I. cf. xanthomelas)*	France	*Salix*	PAM06060405 (LIP), TENN063834	HQ586867		Unpublished

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TABLE 1. (Continued)

Species	Country	Putative host	Voucher	GenBank accession number		Sequence published in
				ITS	LSU	
Inocybe subrimosa (as *I. xanthomelas)*	France	*Quercus, Carpinus*	PAM08082901 (LIP), TENN063832	HQ586856		Unpublished
Inocybe subrimosa (as *I. xanthomelas)*	Sweden		LAS200609	FN550895	FN550895	Ryberg *et. al* 2010
Inocybe subrimosa (as *Inocybe sp1)*	Spain	*Betula alba*	AH 30818	KJ938776		Esteve-Raventós *et al.* 2015
Inocybe subrimosa	**Finland**	**Grass in a garden**	**3223(H) lectotype**	**ON227436**		**This study**
Inocybe substellata	Sweden		EL52-13	KT958927	KT958927	Vauras & Larsson 2016
Inocybe substellata	France.	*Salix herbacea, Polytrichum norvegicum*	Kuhner 73-218 holotype	KT958928		Vauras & Larsson 2016
Inocybe vaurasii	**France**	***Fagus sylvatica***	**AH 48238**	**ON259049**	**ON259049**	**This study**
Inocybe vaurasii	**Sweden**	**Deciduous forest**	**GB-0179884**	**ON227442**	**ON227442**	**This study**
Inocybe vaurasii	**France**	***Fagus sylvatica***	**AH 48140**	**ON259048**	**ON259048**	**This study**
Inocybe vaurasii	**Denmark**	***Fagus***	**EL310-17, GB-0207631**	**ON227440**	**ON227440**	**This study**
Inocybe vaurasii	**Sweden**	**Deciduous forest**	**GB-0129258**	**ON227441**	**ON227441**	**This study**
Inocybe vaurasii	**Sweden**	***Fagus* and *Quercus***	**EL226-11, GB0207630**	**ON227443**	**ON227443**	**This study**
Inocybe vaurasii (as *I. cf. asterospora)*	Sweden.	*Quercus robur*	EL143-05, GB-0207629	AM882722	AM882722	Ryberg *et. al* 2008
Inocybe vaurasii (as *I. xanthomelas*)	Germany	*Corylus avellana*	KR-M-0044910	MT005904		Unpublished
Inocybe vaurasii (as *I. xanthomelas*)	Italy	*Fagus*	16835	JF908163		Unpublished
Inocybe vaurasii	**France**	***Fagus sylvatica***	**AH 47714 holotype**	**ON263162**	**ON276736**	**This study**
Inocybe vaurasii (as Uncultured *Inocybe)*	Spain	*Fagus*	S161	MW282577		Unpublished
*Inocybe vaurasii (*as Uncultured *Inocybe)*	Iran	Enviromental sample. *Fagus, Quercus*	Clone 53	FR852271		Bahram *et al.* 2012
Inocybe xanthomelas	**Spain**	***Fagus sylvatica***	**AH 47646**	**ON263161**	**ON276735**	**This study**
Inocybe xanthomelas (as *Inocybe sp.)*	Germany		DB15-9-15-3-Dondl	MH366571		Bandini *et al.* 2019a
Inocybe xanthomelas	**France**	**Deciduous forest**	**G388214, G00260857 paratype**	**ON227437**		**This study**
Inocybe xanthomelas	**France**	**Deciduous forest**	**G388217, G00260858 paratype**	**ON227439**		**This study**
Inocybe xanthomelas	**France**	**Deciduous forest**	**G388216 "Mail-var. affinis" =G00127626 lectotype**	**ON227438**		**This study**
Pseudosperma flavellum	Sweden		SJ04005	AM882779		Ryberg *et. al* 2008
Pseudosperma spurium	Sweden		SJ92017	AM882784	AM882784	Ryberg *et. al* 2008

FIGURE 1. Most probable tree inferred by Bayesian inference (BI) analysis of the ITS and LSU regions of the rDNA in species of *Inocybe xanthomelas* group. Posterior probability from Bayesian analysis / Bootstrap-ML values around the branches are shown. Thick branches indicate nodes with phylogenetic support in both analysis (bootstrap values ≥ 95% and posterior probability ≥ 0.95). Sequences of *Pseudosperma spurium* and *Pseudosperma flavellum* were used to root the tree. The country of origin of each collection is abbreviated by ISO Alpha-2 codes, with specimens described in this article marked in bold.

Materials and methods

Morphology

The studied collections have been photographed macroscopically in situ with an Olympus OMD E-M5 MarkII digital camera, using tripod and natural light. The macroscopic descriptions are based on fresh material, which was subsequently dehydrated for herbarium conservation. Water and 10–30% ammonia (NH_4OH) were used for microscopic preparations. For the microscopic observations and their corresponding descriptions, a Nikon E200/ Nikon 55i microscope with a Nikon D90 camera, connected to a personal computer, was used. Subsequently, the images taken were processed with a computer program for images (Adobe Photoshop or Lightroom*).* An Index of Slenderness is used, defined as $IS = l^2/d.D$ (Heinemann, 1983), in which *l* is length of stipe, *d* is diameter of stipe and *D* is diameter of pileus. Measurements of microscopic elements were done from calibrated photographs through Piximètre 5.10 R 1541 and then aggregated in a spreadsheet that automatically computes the 5% and 95% percentiles, minimum, maximum, mean (avg), median (M) and standard deviation (SD) for each parameter: [(min–)5%–*avg*–95%(–max)]. Spores measurements include the knobs. Cystidia were measured without crystals and basidia without sterigmata.

The descriptions, both macroscopic and microscopic, were always those observed by the authors for their collections. The material has been deposited in the herbarium of the University of Alcalá (AH), University of Gothenburg (GB) and in the private herbarium of some of the authors (Fermín Pancorbo indicated as FP). The type collections studied were sent on loan from the Herbaria of the Conservatoire et Jardin Botaniques de Genève (G) and the Herbarium of the Botanical Museum of Helsinki (H).

Colour codes are taken from Munsell (1994), terminology follows Vellinga (1998) and Kuyper (1986).

Molecular and phylogenetic analysis

Sequence data for molecular analyses were generated with the aim at placing and present the studied species in a phylogenetic context. At the University of Alcalá de Henares (Spain) the DNA extractions were performed from dried material using a NZY Plant/Fungi gDNA Isolation Kit (NZYTech, Lisboa, Portugal). The amplified regions were the ITS rDNA, which was amplified using primers ITS5 and ITS4 (White *et al.* 1990); and LSU rDNA, which was amplified using primers LR0R and LR5 (Vilgalys & Hester 1990). PCR conditions were as follows: 5 min at 95 °C; 38 cycles of 45 s at 95 °C, 45 s at 52 °C, 1 min at 72 °C; 10 min at 72 °C. Fragments were visualised by electrophoresis on 1% agarose gels, stained with SYBR Safe DNA Gel Stain (Invitrogen by Thermo Fisher Scientific) and visualised with a blue light transilluminator. The amplified samples were purified by precipitation with 4M ammonium acetate, isopropanol and 70% ethanol. Amplicons were sequenced at the Molecular Biology Unit (Faculty of Environmental Sciences, University of Alcalá de Henares) using primers ITS2, ITS3, ITS4 and ITS5 (White *et al.* 1990) for ITS region; and primers LR0R, LR5 (Vilgalys & Hester 1990) and LR21 (Hopple & Vilgalys 1999) for LSU. The consensus ITS and LSU sequences were obtained using Geneious 5.1.7 (https://www. geneious.com). At the University of Gothenburg (Sweden) the ITS and LSU sequence data were generated as described in Nitare *et al.* 2021.To preliminarily verify the identity of the sequences, BLAST searches were performed (Altschul *et al.* 1990).

In total of 23 sequences of the ITS region and 10 of the LSU region were newly generated for this work (Table 1). In order to present species in a phylogenetic context, sequence data were included and assembled from previous studies of *Inocybe* sect. *Marginatae* (Bandini *et al.* 2019a, 2020; Cripps *et al*. 2020; Dovana *et al*. 2020; Esteve-Raventós *et al*. 2015, 2016; Vauras and Larsson 2016). Each ITS sequence type of the new described species were blasted in GenBank (Clark *et al*. 2016) for comparison and the closest records downloaded and included in the data set. Sequences from *Pseudosperma spurium* (Jacobsson & Larsson 2009: 204) Matheny & Esteve-Rav. in Matheny *et al.* (2020: 114) and *Pseudosperma flavellum* (Karsten 1889: 100) Matheny & Esteve-Rav. in Matheny *et al*. (2020: 110) were used as outgroup for rooting of tree.

Sequences were automatically aligned in Aliview (Larsson 2014) and then adjusted manually. All characters of the ITS and LSU regions could be aligned unambiguously. As the phylogenetic inferences did not differ when the ITS1, 5.8S and ITS2 regions were partitioned, the analyses were run without any partition to not over-parameterize them. Alignments were analysed using maximum likelihood (ML) and Bayesian inference (BI) methods. ML analyses were performed in IQTREE web server (Trifinopoulos *et al.* 2016), leaving all other options as default. To determine node support, 1000 ultrafast bootstrap replicates were performed. The substitution model was calculated by ModelFinder implemented in IQ-TREE web server. The best fit model for ML analysis according to BIC was TMP2+F+G4 for ITS region and TN+F+I+G4 for LSU region. BI analysis was performed in MrBayes 3.2.7 (Ronquist *et al.* 2012). The substitution models were sampled within GTR space (Ronquist *et al.* 2012), using two analyses of four MCMC chains

over 20 million generations, starting with a random tree and sampling one tree every 1000 generations. Chains were assumed to converge properly when the standard deviation values of cluster frequencies fell below 0.01 (8886000 generations). A burn-in of 25% of the trees was selected and discarded from each analysis. Branch support (posterior probability values, BPP) was calculated using the consensus tree following the "50% majority rule" of the remaining trees. Nodes with ML bootstrap value >95% and BPP ≥0.95 were considered phylogenetically supported.

Results

The complete aligned ITS and LSU rDNA dataset consisted of 63 taxa and 1724 characters (gaps included). The Bayesian and Maximum Likelihood analyses produced slightly different topologies in the best tree. The main differences were in the positions of the basal branches, however the support on the basal branches were rather low in both analyses. The analyses recovered 13 strongly supported terminal clades and two single branches representing 15 species, *I. xanthomelas, I. phaeocystidiosa* Esteve-Rav., G. Moreno & Bon in Esteve-Raventós & Moreno (1987: 18)*, I. flavobrunnescens* Esteve-Rav., G. Moreno & Bizio in Esteve-Raventós *et al*. (2015: 5)*, I. subrimosa, I. lacunarum* Vauras & E. Larss. (2015: 12)*, I. populea* Takah. Kobay. & Courtec. (2000: 161)*, I. hirculus* Vauras (1995: 156)*, I. antoniniana* E. Sesli, Bandini & Krisai in Bandini *et al.* (2020: 98)*, I. krieglsteineri* Fernández Sas. (2004: 180)*, I. humilis, I. substellata* Kühner (1988: 25)*, I. caprimulgi* Vauras & E. Larss. (2015: 2)*, I. alpinomarginata* C.L. Cripps, E. Larss. & Vauras (2020: 137)*, I. blandula* Bandini, B. Oertel & U. Eberh. (2021: 219) and *I. vaurasii*. In Figure 1, the Bayesian tree is presented with both BPP and MLB values indicated on branches and the position of the new described species *I. vaurasii* is highlighted.

Taxonomy

Inocybe vaurasii Esteve-Rav., E. Larss. & Pancorbo, *sp. nov*. Figs. 2–3

MykoBank no.: MB843429

Etymology:—dedicated to Jukka Vauras from Finland for his valuable contributions to the study of the genus *Inocybe*.

Diagnosis:—*Inocybe vaurasii* has similar morphological characters and habitat to *I. xanthomelas*, such as its slender habit, pale colouration, asteriform spores and preference for Fagaceae forests on limestone soils; the two clearly differ in their ITS data sequences, as well as in the combination in *I. vaurasii* of the more ochre-orange colours of the pileus, larger pleurocystidia (av. 68 × 17.5 µm vs. 54.5 × 15.8 µm), and spores with more prominent knobs (2.2–3.3 vs. 1.2–2.4 µm in height); in BLAST the closest ITS sequences are that of *I. phaeocystidiosa* (87.5 %), as well as *I. blandula* (86.8 %) and *I. alpinomarginata* (86.0 %).

Holotype:—FRANCE. Nouvelle-Aquitaine: Pyrénées-Atlantiques, Osse-en-Aspe. Forêt d'Issaux, under *Corylus avellana* in a *Fagus sylvatica* forest, 43.00222, -0.70667, 917 m asl., 9 October 2016. F. Pancorbo, AH 47714!, GenBank: ITS ON263162, LSU ON276736, *isotypes in* FP16100904!, GB!

Description

Basidiomata agaricoid and stipitate. *Pileus* 20–45 mm diam., not hygrophanous, at first hemispherical to conic-convex, then plano-convex, umbo usually distinctive, broadly conical or shallow, rarely absent; margin slightly incurved when young, finally straight, regular to wavy in old and expanded specimens, sometimes crenulated by remnants of veil; velipellis poorly developed, visible on the umbo in young specimens, arachnoid, whitish, but ephemeral in washed or aged collections; colour uniformly orange-brown when young (Mu 10YR 7/6), becoming ochraceous to chamois towards the margin with age (Mu 5YR 8/8, 2.5GY 8/4); surface dry, smooth, radially fibrose, occasionally subrimose in mature specimens, sometimes showing the presence of remnants of a cobwebby whitish veil. *Lamellae* crowded [L = 42–56; l = (0)–1(–2)], free to hardly adnexed, subventricose, initially whitish, then pale grey (*Psathyrella*-like), later pale-ochraceous to clay-brown, finally tobacco-brown; edge whitish or paler, entire to finely fimbriate. *Stipe*

FIGURE 2. Macroscopic characters of *Inocybe vaurasii*. **a**. Collection AH 47714. Holotype. **b**. Collection AH 48238. **c**. Collection AH 48140. **d**. Detail of velar remains on the pileus. **e**. Collection EL226-11. **f.** Collection EL310-17. **Scale bar**: 20 mm. **Photos**: **a–d** = F. Pancorbo, **e**, **f** = E. Larsson.

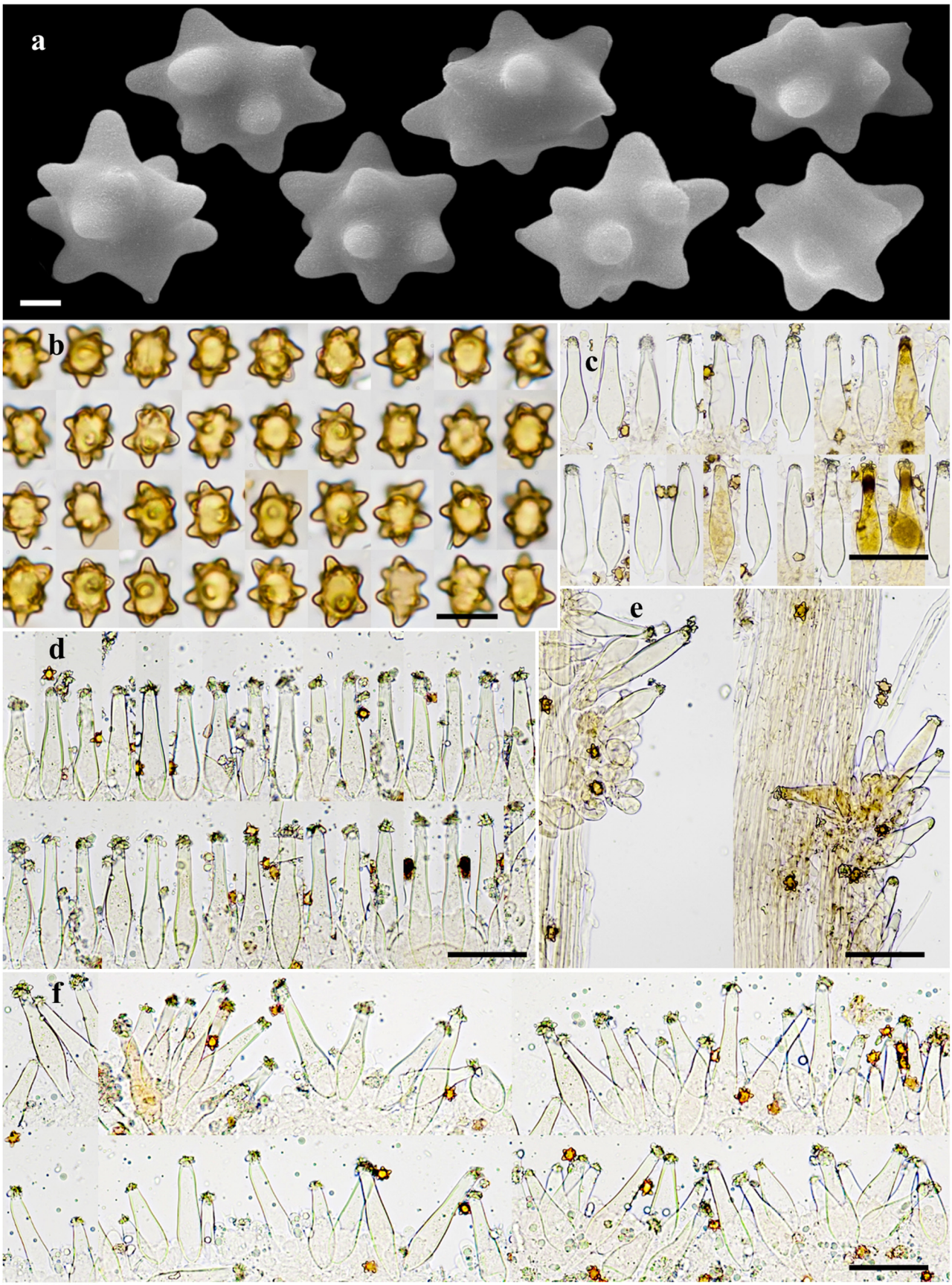

FIGURE 3. *Inocybe vaurasii* (holotype). Micromorphological features. **a.** Basidiospores SEM. **b**. Basidiospores MO. **c.** Pleurocystidia. **d, f.** Cheilocystidia. **e.** Caulocystidia at the base of stipe. **Bar**: 2 µm = **a**; 10 µm = **b**; 50 µm = **c–f**. **Mounting media**: NH_4OH = **b–f**. **Photos**: **a =** G. Moreno; **b–f** = F. Pancorbo.

28–74 × 4–7 mm, fibrose, frequently sinuose and slender, cylindrical, abruptly bulbous towards the base (6–13 mm diam.); colour white when young, darkening with age, finally dark greyish to black; surface densely pruinose along its entire length. *Cortina* not observed. *Context* fibrose, whitish when young, turning dark grey to blackish with age or desiccation. *Odour* not distinctive, taste not significant. Average IS=810.

Basidiospores star-shaped (*Inocybe asterospora*-like), ochraceous, provided with numerous knobs (8–11), 2.2–3.3 µm high, subisodiametric, (8.6–)9.1–*10.8*–12.4(–14.2) × (6.8–)7.7–*8.9*–10.2(–11.8) µm. Q = (1–)1.02–*1.2*–1.39(–1.57) (307 spores from 3 collections). *Basidia* hyaline, claviform, mostly 4-spored, (21.9–)25.5–*28.6*–32(–32.6) × (9.7–)11.2–*12.9*–14.6(–16.8) µm (44 basidia from 1 collection). Gill edge nearly homogeneous and sterile. *Cheilocystidia* (34.6–)44.6–*67.1*–97.7(–108.4) × (13.8–)14.6–*17*–20.5(–21.7) µm (112 cystidia from 3 collections), very abundant, hyaline or showing a ochraceous intracellular pigment, crystalliferous at apex, mostly lageniform, sometimes shortly pedicellate, with very pale yellow reaction to ammonia; *paracystidia* clavate, hyalin. *Pleurocystidia* numerous, similar to cheilocystidia, (44.1–)52.6–*67.9*–83.7(–94.8) × (13.7–)15.5–*17.7*–20.3(–22.2) µm, Q = (2.46–)2.96–*3.8*–5.22(–6.08) (134 cystidia from 3 collections), hyaline or showing a ochraceous intracellular pigment, medium to thick-walled (0.56–)0.83–*1.3*–1.95(–2.03) µm. *Stipitipellis* a cutis of parallel hyphae of 2.8–4.8 µm wide. *Caulocystidia* abundant, lageniform to subcylindrical (30.6–)40.2–*66.8*–86.9(–107.9) × (9.8–)10.5–*14.1*–17.5(–18.2) µm. Q = (1.87–)2.85–*4.8*–7.11(–7.95) (Holotype), present from the apical part to the base of the stipe in tufts, mixed with numerous hyaline piriform to clavate paracaulocystidia, thick-walled. *Clamps* present.

Habitat & Distribution:—*Inocybe vaurasii* is a species with a preference for continental forests of Fagaceae, especially *Fagus sylvatica* in Europe, but also found associated with *Quercus robur* in Sweden; it does not seem to show a marked edaphic preference for soil ph, although most of the studied collections come from calcareous soils or at least more nutrient rich soils. Based on the collections studied and data obtained from GenBank, its distribution area extends throughout humid continental Europe (Germany, Denmark, France, Italy, Spain and Sweden), but it is also known to exist in northern Iran, as shown by GB reference FR852271, which corresponds to the Fagaceae forests of the Hyrcanian Forests (Bahram *et al.* 2012). Some citations refer to *I. xanthomelas* or *I. cf. asterospora*, due to their morphological similarity (see Table 1).

Additional collections examined of Inocybe vaurasii:—DENMARK. Jylland; Midtjylland, Barrit, Staksrode skov, *Fagus* forest on clay and sandy soil, 20 September 2017, E. Larsson EL310-17 (GB-0207631!) (duplicate in AH 56215), GenBank: ITS-LSU ON227440.—FRANCE. Nouvelle-Aquitaine: Pyrénées-Atlantiques, Osse-en-Aspe. Forêt d'Issaux, under *Corylus avellana* in a *Fagus sylvatica* and *Abies alba* forest, 43.00167, -0.70806, 924 m asl., 11 October 2016, F. Pancorbo, AH 48140!, duplicate in FP16101106!, TUR-A!, GenBank: ITS-LSU ON259048; ibidem, on muddy ground under *Fagus sylvatica*, 43.00120, -0.70898, 933 m asl., 13 October 2018, F. Pancorbo, AH 48238!, duplicate in FP18101307!, GenBank: ITS-LSU ON259049.—SWEDEN. Skåne: Sjöbo, Lövestad, Lövestads åsar, in *Fagus* forest, 18 September 1981, Leif & Anita Stridvall, LAS81/325 (GB-0064778!); Skåne: Brunnby, Kockenhus, in deciduous forest, 20 July 2004, K. Bergelin (GB-0179884!), GenBank: ITS-LSU ON227442; Skåne: Andrarum, Christinehofs slottspark, under *Quercus robur*, 21 September 2005, E. Larsson EL143-05 (GB-0207629!), GenBank: ITS-LSU AM882722; Västergötland: Göteborg, Botaniska trädgården, Vitsippsdalen, deciduous forest, 16 September 2006, M. Ryberg (GB-0129258!), GenBank: ITS-LSU ON227441; ibidem, under *Fagus* and *Quercus*, 8 September 2011, E. Larsson EL226-11 (GB-0207630!), GenBank: ITS-LSU ON227443; Halland, Hasslöv, Osbäcks bokskog, 16 September 2009, S. Jacobsson SJ09-028 (GB!).

Inocybe humilis (J. Favre & E. Horak) Esteve-Rav. & Vila, Revista Catalana de Micologia 21: 192 (1998). Figs. 4a, d

≡ *Astrosporina humilis* J. Favre & E. Horak in Horak, Arctic and Alpine Mycology 2: 231 (1987)

Misapplied: *Inocybe humilis* J. Favre, Ergebnisse des Wissenschaftlichen Untersuchungen des Schweizerischen Nationalparks 6: 480, 587 (1960) -inv. art. 40.1-

Studied material: holotype of *I. humilis.* Figs. 5a, b:—SWITZERLAND, God God vers 1800 m prés de S-chanf, Hte Engadine, sur la terre nue graveleuse d'un chemin, foret de mélèzes, d'épicéas, d'aroles (*Pinus cembra*), 5 September 1956, J. Favre, G00126386 (G!), Nº Collector : Z.S. 583. GenBank: ITS ON227435.

Basidiospores star-shaped (*Inocybe asterospora*-like), ochraceous, provided with numerous knobs (8–12), 1.2–2.5 µm high, subisodiametric, (9–)9.1–*9.9*–10.7(–11) × (7–)7–*7.5*–8(–8) µm. Q = (1.2–)1.2–*1.3*–1.4(–1.4) (12 spores). *Basidia* hyaline, claviform, 4-spored. Gill edge heterogeneous. *Cheilocystidia* (45–)45–50.3–55(–55) × (14–)14.7–17.6–19.7(–20) µm (6 cystidia), abundant, hyaline or showing a golden intracellular pigment, crystalliferous at apex, mostly lageniform, sometimes shortly pedicellate, with pale yellow reaction to ammonia; *paracystidia* clavate, hyalin.

Pleurocystidia numerous, similar to cheilocystidia, (44.1–)52.6–*67.9*–83.7(–94.8) × (13.7–)15.5–*17.7*–20.3(–22.2) µm, Q = (2.46–)2.96–*3.8*–5.22(–6.08) (6 cystidia), hyaline or showing a golden-brown intracellular pigment, thick-walled (2–3) µm. *Trama* of stipe quite yellow, just darkening to brownish yellow. *Caulocystidia* abundant, lageniform to subfusiform (31.5–)32.5–*52.2*–63(–65) × (13–)14.4–*18*–22.2(–23) µm. Q = (1.87–)1.95–*2.9*–3.9(–4.01) (11 cystidia), weakly crystalliferous, present from the apical part to the base of the stipe in tufts, where they appear mixed with cylindrical caulocystidiod hairs and with numerous hyaline clavate paracaulocystidia, thick-walled. *Clamps* present.

FIGURE 4. Fresh basidiomata *in situ.* **a, d.** *Inocybe humilis* AH 56423. **b, e.** *Inocybe xanthomelas* AH 47646. **c, f.** *Inocybe subrimosa* AH 44474. **Scale bar**: 20 mm. **Photos**: F. Pancorbo.

Additional collections examined of Inocybe humilis:—SPAIN, Girona, Ulldeter, Setcases (Ripolles), UTM 4384697, 2300 m asl., in *Salix herbacea* and *S. retusa*, 14 August 1997, J. Vila, AH 23498!, duplicate in JVG970814-14, GenBank: ITS-LSU ON259052; Madrid, Somosierra, Dehesa Boyal, under *B. pendula*, *Corylus avellana*, 13 July 1988, G. Moreno, F. Esteve-Raventós, AH 46520!; ibidem, under *B. pendula*, *Q. petrea*, *S. atrocinerea*, 1 September 2001, M. Villarreal, F. Esteve-Raventós, AH 26954!, GenBank: KJ938773 (as *I. xanthomelas*); ibidem, La Hiruela, under *Betula pendula*, 14 July 2002, J.C Campos, J.P. Campos, AH 29895!, GenBank: KJ938774 (as *I. xanthomelas*); ibidem, Rascafría, Arroyo de la Angostura, 40.835642, -3.897870, 1328 m, under *Pinus sylvestris*, *Betula alba*, *Salix* sp., 5 August 2007, F. Pancorbo, AH 56428!; ibidem, on the margin of a peat bog under *B. alba*, *P. sylvestris*, 27 June 2009, F. Pancorbo, AH 56429!; ibidem, 2 July 2011, F. Pancorbo, AH 45142!, GenBank: ITS-LSU ON259050; ibidem, El Brezal, 40,858859, -3,909738, 1236 m asl., on the margin of a peat bog under *B. alba*, *P. sylvestris*, 6 August 2011, F. Pancorbo, AH 56430!; ibidem, Arroyo de La Angostura, 40.83564298,-3.89787044, 1340 m asl., On the margin

of a peat bog under *B. alba*, *P. sylvestris*, *Salix* sp., 23 June 2012, F. Pancorbo, AH 45147!; ibidem, 30 June 2012, F. Pancorbo, AH 45144!, GenBank: ITS-LSU ON259051; ibidem, 7 July 2013, F. Pancorbo, AH 40430!, GenBank: KJ938775 (as *I. xanthomelas*); ibidem, 14 July 2013, F. Pancorbo, AH 56424!; ibidem, 14 July 2013, F. Pancorbo, AH 56425!; ibidem, 1 August 2013, F. Pancorbo, AH 56426!; ibidem, 3 July 2015, F. Pancorbo, AH 56427!; ibidem, 14 August 2015, F. Pancorbo, AH 47700!; ibidem, Arroyo Aguilón, 40.877638, -3.877161, 1180 m asl., on the margin of a brooklet in a *Quercus pyrenaica* forest, on acidic soil, 10 July 2017, F. Pancorbo, AH 56431!; ibidem, 26 September 2017, F. Pancorbo, AH 48192!, GenBank: ITS-LSU ON259053; ibidem, Arroyo de La Angostura, 40.83611, -3.89667, 1337 m asl., on the margin of a peat bog under *B. alba*, *P. sylvestris*, 30 June 2018, F. Pancorbo, AH 48220!; ibidem, 24 June 2020, F. Pancorbo, AH 56356!; ibidem, 24 June 2020, F. Pancorbo, AH 56357!; ibidem, 3 August 2020, F. Pancorbo, AH 56364!, GenBank: ITS-LSU ON263577; ibidem, 13 August 2020, F. Pancorbo, AH 56370!; ibidem, 10 July 2021, F. Pancorbo, AH 56417!; ibidem, 21 August 2021, F. Pancorbo, AH 56423!, GenBank: ITS ON263163. SWEDEN, Västergötland, Alingsås, Nolhagaparken, under *Fagus* and *Quercus*, 15 August 2004 (GB!), GenBank AM882718; ibidem, under *Fagus* and *Quercus*, 8 September 2015, E. Larsson 143-15 (GB!); Jämtland, Bräcke, Bräcke kyrkogård, under *Pinus sylvestris*, 27 August 2018, E. Larsson 226-18 (GB!).

Inocybe subrimosa (P. Karst.) Sacc., Sylloge Fungorum 9: 100 (1891). Figs. 4c, f

≡ *Clypeus subrimosus* P. Karst., Meddelanden af Societas pro Fauna et Flora Fennica 16: 38 (1888)

Studied material: lectotype of *I. subrimosa* (as *Clypeus subrimosus*) invalidly designated by S. Huhtinen & J. Vauras in 2019 (unpublished) and validated here (MBT: 10007880). Figs. 5c, d:—FINLAND, Tavastia australis, Tamela, Mustiala, Runkomäki, *Locis declivibus graminosis in horto Mustialensis*, 15 September 1888, *leg*. & *det*. P.A. Karsten, P.A.K. No. 3223 (H!), GenBank: ITS ON227436; ibidem, P.A.K. No. 3224 (H!), paratype.

Basidiospores star-shaped, ochraceous, provided with numerous knobs (9–12), 1.2–2.8 µm high, subisodiametric, (9.2–)10.2–*11.2*–12.3(–12.4) × (7.7–)8–*8.8*–9.5(–10.3) µm. Q = (1.1–)1.1–*1.2*–1.38(–1.4) (41 spores). *Basidia* hyaline, claviform, 4-spored. *Cheilocystidia* (48.2–)50.6–*61.6*–72.5(–74.9) × (17.2–)17.3–*18.9*–21.4(–21.6) µm, Q = (2.58–)2.6–*3.2*–4.09(–4.34) (11 cystidia), abundant, hyaline or showing a golden intracellular pigment, crystalliferous at apex, mostly lageniform, sometimes shortly pedicellate, with a shiny yellow reaction to ammonia; *paracystidia* clavate, hyalin. *Pleurocystidia* numerous, similar to cheilocystidia, (50.8–)51.5–*62.3*–69.7(–75) × (11.7–)13–*16.5*–20.5(–22) µm, Q = (2.8–)3.0–*3.8*–4.9(–5.3) (16 cystidia), hyaline or showing a golden-brown intracellular pigment, thick-walled (1.5–3.5 µm.) Hymenophoral *Trama* quite yellow. *Caulocystidia* abundant, lageniform to subfusiform (36.7–)41.4–*54.7*–68.4(–71.5) × (13.1–)13.6–*16.4*–19.5(–20.9) µm, Q = (2.31–)2.56–*3.3*–4.66(–5.1) (21 cystidia), crystalliferous, present from the apical part to the base of the stipe in tufts, with numerous hyaline clavate paracaulocystidia. *Clamps* present.

Additional collections examined of Inocybe subrimosa:—SPAIN, Madrid, Bustarviejo, Puerto de Canencia, under *Betula alba*, *Pinus sylvestris*, October 1975, C. Lado, AH 01210!; ibidem, 17 June 1976, C. Navarro, G. López, G. Moreno, AH 00630!; ibidem, *Betula alba*, 8 July 1977, C. Lado, G. Moreno, AH 09323; ibidem, *Betula alba*, 10 August 1977, J.M. Barrasa, G. Moreno, AH 09324! GenBank: ITS ON259056; ibidem, Somosierra, Dehesa boyal, under *Betula alba*, 13 July 1988, G. Moreno, F. Esteve-Raventós, AH 29921!; ibidem, Bustarviejo, Puerto de Canencia, under *Betula alba*, 26 June 1992, M. Heykoop, F. Esteve-Raventós, AH 24635!; ibidem, 2 July 1992, J. Rejos, F. Esteve-Raventós, AH 24977!; ibidem, Somosierra, Dehesa Boyal, *Betula alba*, 30 June 1993, R. Valenzuela, F. Esteve-Raventós, AH 22147!; ibidem, Bustarviejo, Puerto de Canencia, under *Betula alba*, *Pinus sylvestris*, 2 June 1994, V. González, F. Arenal, F. Esteve-Raventós, AH 15695!; ibidem, AH 15697; ibidem, 28 May 1997, V. González, M. Villarreal, F. Esteve-Raventós, AH 22133; ibidem, Somosierra, Dehesa Boyal, 29 May 1997, M. Villarreal, C. Sánchez, F. Esteve-Raventós, AH 22154; ibidem, Bustarviejo, Puerto de Canencia, under *Betula alba*, 28 June 2003, J.C Campos, J.P. Campos AH 30818! GenBank: ITS KJ938776 (as *Inocybe* sp.); ibidem, Rascafría, Arroyo del Paraje, 40,831224, -3,892679, 1420 m asl., under *Betula alba*, 16 June 2007, F. Pancorbo, AH 44474!, GenBank: ITS-LSU ON259054; ibidem, Arroyo de La Angostura, 40.835642, -3.897870, 1272 m asl., under *Betula alba*, 30 June 2007, F. Pancorbo, AH 44475!, GenBank: ITS-LSU ON259055; ibidem, under *Betula alba, Pinus sylvestris*, 11 June 2011, F. Pancorbo, AH 45141!; ibidem, AH 56399!; ibidem, AH 56400! SWEDEN, Jämtland, Lockne, Storvålen, under *Pinus* and *Picea*, 27 August 2018, E. Larsson 224-18 (GB!); Västergötland, Alingsås, Erska, Gräfsnäs slottsruin, under deciduous trees, 22 July 1980, L. & A. Stridvall LAS80/134 (GB-0064775!).

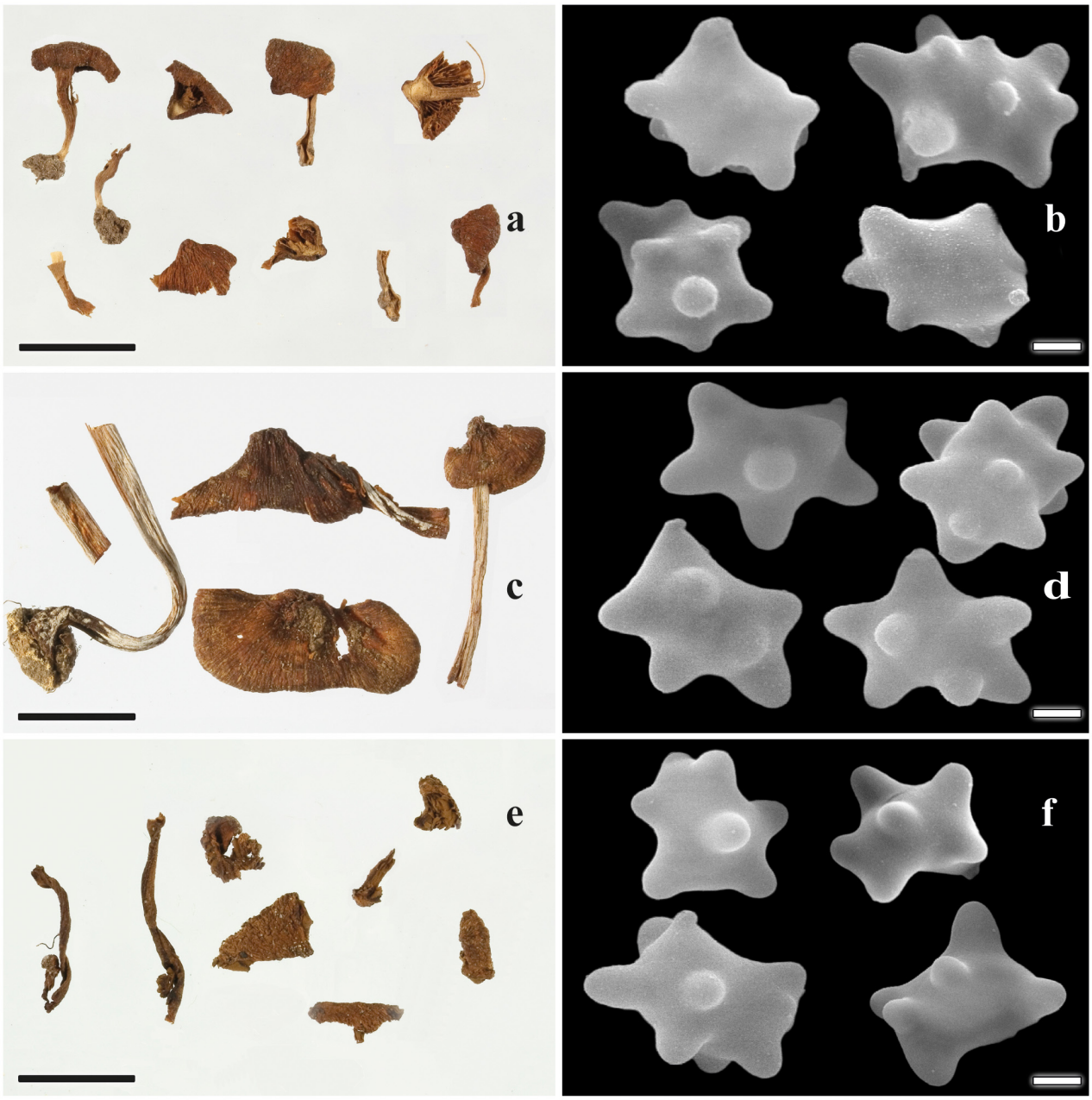

FIGURE 5. Vouchers and SEM spores of types. **a, b.** *Inocybe humilis* J. Favre, G00126386, Z.S. 583. Holotype. **c, d.** *Inocybe subrimosa* (P. Karst.) Sacc. P.A.K. No. 3223 (H). Lectotype. **e, f.** *Inocybe xanthomelas* Boursier & Kühner, « Mail var. affinis » G00127626. Lectotype. **Scale bar**: 2 µm = **b**, **d**, **f**; 10 mm = **a**, **c**, **e**. **Photos**: G. Moreno.

Inocybe xanthomelas Boursier & Kühner in Kühner, Bulletin de la Société Mycologique de France 49: 84 (1933). Figs. 4b, e

Studied material: lectotype of *I. xanthomelas* invalidly designated by J. Vauras in 2007 (unpublished) and validated here by Vauras & Esteve-Raventós (MBT: 10008763). Figs 5e, f:—FRANCE, Seine-et-Marne, Fontainebleau, Mail (1 ex), a terre ou dans les feuilles mortes des bois feuillus (hêtres) ou mêlés, 19 August 1931, R. Kühner, « Mail var. affinis » G00127626 (G!), GenBank: ITS ON227438; paratype of *I. xanthomelas,* Seine et Marne, Fontainebleau, près de Mail, 6 August 1930, R. Kühner, Herb. Kühner « Nedler » G00260857, GenBank: ITS ON227437; paratype of *I. xanthomelas,* Seine et Marne, Fontainebleau, Mail Henry IV, 19 August 1931, R. Kühner, Herb. Kühner « Mail-var. Amphi » G00260858. GenBank: ITS ON227439.

Basidiospores star-shaped, ochraceous, provided with numerous knobs (8–15), 1.2–2.4 µm high, subisodiametric, (9.1–)9.4–*10.6*–11.9(–13.1) × (7.1–)7.5–*8.1*–8.8(–9) µm. Q = (1.16–)1.18–*1.3*–1.4(–1.5) (40 spores). *Basidia* hyaline, claviform, 4-spored. Gill edge more or less the same colour as the faces (due to brownish content). *Cheilocystidia*

(46.4–)46.7–*49,3*–52(–52.3) × (13.2–)13.4–*14.6*–15.7(–15.8) µm. Q = (3.1–)3.1–*3.4*–3.7(–3.72) (10 cystidia), very frequent, well differentiated, hyaline or showing a brownish intracellular pigment, crystalliferous at apex, lageniform, with prominent neck; *paracystidia* clavate, hyalin. *Pleurocystidia* numerous, similar to cheilocystidia, (50–)50–*59*–71.4(–78) × (14–)14.2–*16.9*–19.4(–20) µm. Q = (2.94–)2.97–*3.5*–4.26(–4.58) (12 cystidia), hyaline or showing a brownish intracellular pigment, thick-walled (2.3–2.5 µm), with very pale-yellow reaction to ammonia. *Caulocystidia* very abundant, lageniform with well delimited neck (41–)44.1–*54.2*–62.2(–63.4) × (14.7–)14.7–*15.5*–16.7(–16.9) µm. Q = (2.72–)2.81–*3.4*–4.1(–4.14) (7 cystidia), with dark brown content, crystalliferous, present from the apical part to the base of the stipe in tufts, with numerous hyaline clavate paracaulocystidia. *Clamps* present.

Additional collections examined of Inocybe xanthomelas:—SPAIN, Huesca, Bielsa, La Larri, in a *Fagus sylvatica* forest on calcareous soil, 42.681666, 0.078888 , 1305 m asl., 25 August 2015, M.A. Ribes, J. Hernanz, F. Esteve-Raventós, F. Pancorbo, AH 47646!, GenBank: ITS ON263161-LSU ON276735; ibidem, 12 October 2018, F. Pancorbo, AH 48233! SWEDEN, Gotland, Fardhem, Fardhem prästänge, under *Tilia* and *Corylus*, 13 September 2017, E. Larsson 485-17 (GB!); Öland, Torslunda, Skogsby, Tveta hägnet, 29 August 2005, T. Knutsson 2005-024 (GB-0234342!).

Discussion

A comparative study of *Inocybe vaurasii* has been made with three other apparently similar species, *I. xanthomelas*, *I. humilis* and *I. subrimosa*. Because of the marked darkening of the context with age or dehydration, they all belong to the Xanthomelas group (section *Marginatae* Kühner) and share the particular asteriform morphology of their spores. At the micro-morphological level, this character can generate confusion when recognizing them, and in fact there are a number of erroneous determinations of collections deposited in GenBank and UNITE, identified as *I. xanthomelas*. To resolve this issue, type material of these three species has been studied and we were able to generate the ITS region for all of them, fundamental to clarify their taxonomic relationships and rule out possible misinterpretations as has happened in the past.

According to the phylogenetic analyses carried out, the four species compared do not seem to be closely related to each other in the Xanthomelas group (see Fig. 1). The species after which the group is named, *I. xanthomelas*, seems to occupy a rather isolated position with respect to the others. The macroscopic appearance of *I. xanthomelas* is very similar to that of *I. vaurasii*, both having a gracile appearance (IS = 761–810), medium size of the basidiomata and a well-defined bulb at the base, although not marginate. In *I. xanthomelas* there is a very marked darkening of the basidiomata with age or dehydration, the stipe is originally white and takes on greyish and finally practically blackish tones diagnostically (Esteve-Raventós *et al*. 2015). In *I. vaurasii* the ochraceous-brown tones are more evident in the pileus and the stipe darkens to a dark orange-brown, never grey before blackening. The cystidia and spores of both species, as reflected in the diagnosis of *I. vaurasii*, show differences in size of cystidia and height of spore ornamentation. According to the data analysed, *I. xanthomelas* is a much less frequent species than *I. vaurasii*. We only know that it has been determined with certainty through a sequence deposited in GenBank by Bandini (MH366571) [see *Inocybe xanthomelas* in web page *Inocybe. org.*, available from: https://www.inocybe.org/genus-inocybe-höckersporer/xanthomelas/ (accessed: 04 May 2022)]; found twice at the same locality in the Aragonese Pyrenees, under *Fagus* in limestone soils (Pancorbo *et al*. 2017: 38), and from the calcareous islands Gotland and Öland in Sweden under *Corylus*, *Tilia* and *Quercus*.

Inocybe humilis was originally described in a subalpine habitat, under conifers (Favre 1960). However, it can also fruit in alpine areas with dwarf willows (Horak 1987, Esteve-Raventós & Vila 1998). As its name “humilis” = small/humble indicates, the fructifications of this species are always rather small in size and show a yellowish-brown colouration that is already evident when young, with a pileus that tends to break into rather small, appressed scales. Some sequences deposited in GenBank appear with the epithet *I. straminipes* Romagn. (1979: 362), probably because of the yellowish colouration of the stipe with development, although the latter species turns out to be a synonym of *I. salicis* Kühner (1956: 175) (Vauras & Kokkonen 2009: 66, Esteve-Raventós pers. obs. PC!, G!). In *I. humilis* the adult specimens yellow or brown slightly, but never darken or blacken markedly in exsiccatum. The spores are somewhat smaller in size than in the other species discussed here (9–)9.1–*9.9*–10.7(–11) × (7–)7–*7.5*–8(–8) µm, isodiametric, but also sometimes with a certain sub-isodiametric tendency (Qm = 1.3), with well–marked, but sometimes somewhat irregularly high nodules, 1.2–2.5 µm (see Fig. 5b). Phylogenetically *I. humilis* occurs in the subgroup krieglsteinerii (see Fig. 1), whose species show generally elongate and narrow cystidia on the stipe and hymenium, often provided with a characteristic microcrystalline cap. Both show clear differences in their ecological preferences, with *I. krieglsteineri*

being a clearly mesophilic species with a preference for deciduous forests, although in the Iberian Peninsula it also grows in natural or reforested mixed forests (Fernández-Sasia 2004; Pancorbo *et al*. 2015: 202), in acidic sandy soils. *Inocybe villosa* Bandini, B. Oertel & U. Eberh. in Bandini *et al.* (2019b: 285), which also belongs to this group, is a hygrophilous species, fruiting in very humid riparian forests (*Salix*, *Alnus*, *Betula*), with a rather similar ecology to *I. humilis*, but its spores are clearly heterodiametric and provided with few nodules, sometimes with a marked polygonal outline. Our revision of the holotype of *Inocybe concinnula* J. Favre (1955: 201) turned out to represent a species most similar to *I. villosa*, since the two hardly differ in their morphological characters. The holotype of *I. concinnula*, however, comes from alpine areas under dwarf willows.

A fourth species included in this review is *Inocybe subrimosa*, which can also be confused morphologically with *I. xanthomelas* or *Inocybe asterospora* Quél. It was originally described by Karsten (1888) from grassy gardens (urban areas) in Mustiala (Finland), and we have studied the two original collections. Of these, one was invalidly designated as a lectotype by S. Huhtinen and J. Vauras in 2019, as it was annotated on the envelope (H). After our revision, we confirmed that both collections (syntype) represent the same species, and the lectotype designation is validated in this contribution. According to the sequences of our phylogenetic study that match that of the lectotype, this species seems to show a wide distribution in humid deciduous forests, both mesophilic and montane in Europe (Finland, Sweden, France, Spain...), although it does not seem to be frequent. The typical isodiametric and asteriform spores with numerous very conspicuous nodules (–2.8 µm high) are very similar to those of *I. asterospora* Quél. (1879: 50) The macroscopic appearance of the adult and aged basidiomata of *I. subrimosa* is very reminiscent of that of *I. asterospora*, due to the dark brown stipe colouring and the rimose appearance of the pileus margin. A simple observation of the original colour of the stipe in both species, whitish in *I. subrimosa*, is sufficient to avoid confusion between the two taxa. We have found *I. subrimosa* abundant in Spain in very humid montane forests, with presence of *Pinus*, *Betula* and *Salix*, always in acidic soils. The collections from Sweden have been found under both coniferous and deciduous woods. *Inocybe subrimosa* shows some phylogenetic relationship with *I. obtusiuscula* Kühner (1988: 23) [= *I. rufofusca* (Favre 1955: 119) Bon (1997: 105)] and the North American species *I. intricata* Peck (1909: 36) (see Esteve-Raventós *et al*. 2015: Fig. 4).

Two species with asteriform spores, *I. substellata* and *I. undinea* Bandini, P.-A. Moreau & B. Oertel in Bandini *et al*. (2019: 1115), were the subject of a previous study by other authors, and for which sequences of the type material are available. The former corresponds to an alpine species growing under dwarf willows (Kühner 1988, Vauras & Larsson 2016), phylogenetically related to *I. caprimulgi*, and showing large spores (9.5–*11*–12.8 × 7.2–*8.5*–10 µm, holotype G!) with a substellate, appearance. *Inocybe undinea* is associated with *Alnus*, in mesophilic environments and acid soils; it is characterized by asteriform spores with very prominent nodules and by cystidia with a narrow and elongated neck (Bandini *et al*. 2019a; Esteve-Raventós *et al*. ined.). Both species are not phylogenetically much related to *I. vaurasii* or to the rest of the species discussed here (see Fig. 1).

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