A revision of the *Inocybe grammata* group in North America including four new taxa

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Abstract. A systematic revision of North American species with morphological similarities to *Inocybe grammata* was conducted based on materials collected in eastern and western North America and Central America. Eight taxa are confirmed in the group proposed here as *I.* sect. *Albodiscae* sect. nov., species of which are often characterized by a bicolorous pileus with a distinct pallid disc, the margin covered with superficial silky fibrils, entirely pruinose stipe with a slight or obvious marginate bulbous base, angular to angular-nodulose basidiospores with comparatively few nodules, and thick-walled cystidia. Species in the section are mainly distinguished by basidiome size, pileus color and texture, variation in basidiospore length and number of nodules, to some extent geographic location, and plant association. The section includes the widely distributed *I. grammata* (= *I. albodisca*), which associates with conifers and birch in eastern North America; *I. albodiscoides* sp. nov. from the Pacific Northwest, previously subsumed under *I. grammata* and *I. albodisca*; *I. floridana* from northern Florida, reported for the first time in more than 75 years; *I. acriolens*, an apparent associate of hemlock and pine in southeast Canada and the northeast U.S.; *I. grammatoides*, an aspen associate in northern regions of the U.S. and southeast Canada; *I. velicopia* sp. nov., a widely distributed associate of oak and chestnut in the eastern U.S. and Costa Rica; *I. panamica* sp. nov. from oak and oak-*Oreomunnea* (Juglandaceae) forests in Costa Rica and Panama; and *I. vestalis*, a European species sister to the rest of sect. *Albodiscae* but lacking the distinct bicolored pileus. Independent phylogenies of ITS+28S, *rpb2*, and *rpb1* are inferred. Taxonomic descriptions, illustrations, and/or notes of the North American taxa are provided.

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Resumen. Se realizó una revisión sistemática de las especies de América del Norte con similitudes morfológicas con *Inocybe grammata* con base en materiales recolectados en el este y oeste de América del Norte y América Central. Se confirman ocho taxones en el grupo propuesto aquí como ***I.* secc. *Albodiscae* secc. nov.**, especies que a menudo se caracterizan por un píleo bicolor con un disco pálido distintivo, el margen cubierto con fibrillas sedosas superficiales, estípite completamente pruinoso con una base bulbosa marginada leve u obvia, basidiosporas angulares a nodulosas angulares comparativamente con pocos nódulos, y cistidios de paredes gruesas. Las especies de la sección se distinguen principalmente por el tamaño del basidioma, el color y la textura del píleo, la variación en la longitud de las basidiosporas y el número de nódulos y hasta cierto punto la ubicación geográfica y el tipo de plantas a la que se asocian. La sección incluye *I. grammata* (= *I. albodisca*) que es ampliamente distribuida y se asocia con coníferas y abedules en el este de América del Norte; ***I. albodiscoides* sp. nov.** se encuentra en el noroeste del Pacífico y que anteriormente era incluida en *I. grammata* e *I. albodisca*; *Iais floridana* del norte de Florida que se registra por primera vez en más de 75 años; *I. acriolens*, una especie aparentemente asociada a abetos y pinos en el sureste de Canadá y el noreste de los EE. UU.; *I. grammatoides*, asociado a álamos en las regiones del norte de los EE. UU. y el sureste de Canadá; *I. velicopia* sp. nov., asociada a robles y castaños y ampliamente distribuida en el este de los EE. UU. y Costa Rica; ***I. panámica* sp. nov**. de bosques de roble y roble-*Oreomunnea* (Juglandaceae) en Costa Rica y Panamá; e *I. vestalis*, una especie europea hermana del resto de la sect. *Albodiscae* pero sin el píleo bicolor distintivo. Se infieren filogenias independientes de ITS+28S, *rpb2* y *rpb1* y se proporcionan descripciones taxonómicas, ilustraciones y/o notas de los taxones de América del Norte.

Inocybe grammata Quél. was described in the late nineteenth century from sandy birch woods in northern France with a creamy pileus center, the presence of silvery fibrils on the darker pileus margin, a noticeably pruinose white stipe with a rose tint and bulbous base, rather unpleasant odor, and angular basidiospores (Le Breton & Quélet, 1879). No physical type specimen exists, but the species was lectotypified by Vauras (1997) with a painting affiliated with the protologue. Some 20 years later the very similar *I. albodisca* Peck was described from New York (Peck 1898). In a detailed morphological study, Vauras (1997) reviewed the taxonomic history of *I. grammata* concluding that specimens ascribed to *I. albodisca* from throughout North America were synonymous with *I. grammata*. *Inocybe grammata* is characterized microscopically by the presence of thick-walled cystidia and somewhat small nearly angular spores with relatively few or obscure nodules (Vauras, 1997). The species is suggested to have a broad Holarctic distribution occurring on a wide range of soils varying in pH under *Betula*, *Pinus*, and in alpine areas with dwarf *Salix* (Vauras, 1997; Jacobsson & Larsson, 2012). Taxonomic treatments have placed *I. grammata* in *I.* sect. *Marginatae* Kühner (Kühner, 1933; Singer, 1986; Bon, 1998; Jacobsson & Larsson, 2012), but several phylogenetic studies have shown that species of sect. *Marginatae*, typified by *I. asterospora* Quél., do not form a monophyletic group (Matheny, 2005; Matheny et al., 2009; Ryberg et al., 2010; Dovana et al., 2020). In a multigene phylogenetic study by Ryberg et al. (2010), *I. grammata* was recovered as sister to the rest of what is now recognized (see Matheny et al., 2020) as the genus *Inocybe* but with poor support. In Europe four additional species have been described that share some affinities with *Inocybe grammata*. These include *I. pargasensis* Vauras (Vauras, 1997), *I. entolomatospora* Bidaud, Ferville & Armada (Bidaud et al., 2012), *I. grammatoides* Esteve-Rav., Pancorbo & E. Rubio (Crous et al., 2019), and *I. vestalis* Bandini, Weholt & B. Oertel (Bandini et al., 2020). DNA data are currently only available for two of these species (*I. grammatoides* and *I. vestalis*), which supports their autonomy, but no phylogenetic study of any of them has been presented. In North America *I. albodisca*, described originally from New York, and *I. acriolens* Grund & D.E. Stuntz and *I. permucida* Grund & Stuntz, both described from Nova Scotia, have been suggested as allies of *I. grammata*, and one of them, *I. albodisca*, has been synonymized with *I. grammata* based on morphological similarity (Kühner, 1933; Vauras 1997). Others have maintained their separation (e.g., Bon, 1998). Here we document recent collections of these species from North and Central America to gain a better understanding, taxonomically and systematically, of the species-level diversity present in the *Inocybe grammata* group. Our work establishes the conspecificity of multiple eastern North American taxa with *I. grammata* but also distinguishes other taxa including three new species and confirms the presence of *I. grammatoides* from North America for the first time. We do this considering comparisons of morphology, ecology, geographic distribution, and analyses of separate gene trees. In addition, we produce molecular annotations of the types of *I. acriolens* and *I. permucida* to aid in their assessment, and document *I. floridana* for the first time since it was first described in the 1940s. Taken together these taxa are placed in a new section of *Inocybe*, *I.* sect. *Albodiscae*.

Materials and methods

Field Collections

Specimens were collected in the field and notes on gross morphology taken when fresh. Colors were approximated or compared using the Munsell Soil Color Charts (1954), Kornerup and Wanscher (1967), and Ridgway (1912). Color notations from the latter texts are placed in parentheses in the taxonomic descriptions below. For some collections fresh tissues were treated with para-dimethlyaminobenzaldehyde (PDAB) (Matheny et al., 2013), and 5% KOH was applied to the pileus surface to note any macrochemical reactions. Materials were then dried on a food dehydrator for preservation. Sections were made by hand with a razor and mounted in 5% KOH to study anatomical features on a Nikon i80 Eclipse light microscope. Measurements of basidiospores and other microscopic features (terminology following Kuyper (1986)) were conducted using Elements D software (Nikon Instruments Inc., Melville, New York). Basidiospore dimensions in excess of two standard deviations from the mean are placed in parentheses. The number of basidiospores (n) measured and number of collections from which they were made (x) are indicated as (n/x). Average basidiospore dimensions and Q values are italicized. Q values indicate the quotients or lengths divided by widths of spores in profile view. Line art was prepared following Braaten et al. (2014). Dried materials were accessioned at the following herbaria: CSU, TENN, UCH, and WTU. Additional collections were borrowed from ACAD, FLAS, and NY. Herbarium codes follow Thiers (2022, updated continuously). Select collections of L.V. Kudzma reside in a personal herbarium at a private residence maintained in Annandale, New Jersey. Reference to "pers. herb." Under specimens examined refers to these collections.

DNA Extraction, PCR, and Sequencing

Most DNA extractions were performed using an E.Z.N.A. fungal DNA extraction kit (Omega Bio-Tek, Norcross, Georgia). For recent collections made during the past four years, samples of lamellar fragments were placed in 40 uL of Extract-N-Amp solution (Signa-Aldrich, St. Louis, Missouri), stored at room temperature for at least 10 mins, incubated at 95 C for 10 mins, then treated with an equal volume of 3% bovine serum albumin (BSA) dilution solution (Truong et al., 2017). DNA from historical type and ancillary collections was extracted using a High Performance or 'HP' fungal DNA extraction kit (Omega Bio-Tek, Norcross, Georgia). Protocols for PCR, clean-up, and sequencing are provided in Sánchez-García et al. (2014).

We sequenced two different gene regions of nuclear rDNA (ITS and the 5-prime end of the 28S gene region), the most variable region of *rpb2* between conserved domains 6 and 7, and the highly variable region of *rpb1* between conserved domains A and C. A total of four loci were studied. Primers for ITS included ITS1F/ITS4 and/or ITS1F/ITS2 and 5.8SR/ITS4 (White et al., 1990). Primers for 28S included LR0R/-LR7, using LR5 as an internal sequence primer, or LR0R/LR16 (Vilgalys & Hester, 1990; Cubeta et al., 1991) for types and other historical collections. Primers for *rpb2* included b6F and b7.1R (Matheny, 2005) or f5F (Liu et al., 1999) paired with b7.1R. The region of *rpb1* was amplified typically using primers gAf (Stiller & Hall, 1997) and fCr (Matheny et al., 2002) and sequenced using the additional primers int2F, int2.1F, and/or int2.1R (Frøslev et al., 2005). On occasion the primer aB-rev from Matheny et al. (2002) was used for amplification and sequencing. Amplicons were sequenced at the University of Tennessee Genomics Core facility on an Applied Biosystems 3730 Analyzer and chromatograms inspected using Sequencer 5.0.1 (Gene Codes Corp., Ann Arbor, Michigan). Sequences of material identified in the personal herbarium of L.V. Kudzma were generated following Matheny and Kudzma (2019). Sequences were submitted to GenBank (Table 1).

Phylogenetic Analyses

Three alignments were assembled: the first, a combined alignment of ITS and 28S nucleotide sequences, the second, an *rpb2* nucleotide alignment, and the third, an *rpb1* nucleotide alignment. For taxon sampling of the first dataset, we performed BLASTn searches with ITS data produced from our collected materials and reference sequences from prior studies (Crous et al., 2019; Bandini et al., 2020) at NCBI during Mar 2022 and downloaded ITS sequences with >92% similarity and an E value of 0. Taxon sampling of *rpb2* was based on Matheny and Kudzma (2019), which presented a phylogenetic analysis of 782 Inocybaceae *rpb2* sequences. The latter then guided taxon selection for the *rpb1* alignment. Member(s) of the *Inocybe soluta* Velen. Clade, including *I. stellatospora* (Peck) Massee, and samples of *I. sindonia* (Fr.) P. Karst. were chosen as outgroups based on Ryberg et al. (2010) and Matheny and Kudzma (2019).

Sequences of ITS and 28S were initially aligned in ClustalX 2.0.9 (Larkin et al., 2007), refined in AliView 1.11 (Larsson, 2014), and saved as nexus files. The *rpb2* and *rpb1* alignments were pruned to relevant ingroup taxa and outgroups from carefully curated but unpublished inclusive datasets maintained by the lead author. All sites in each dataset were included in phylogenetic analyses. Alignments were converted to phylip format, where necessary, and analyzed under the maximum likelihood (ML) criterion using RaxML 8.2.9 (Stamatakis, 2014) and Bayesian inference (BI) using MrBayes 3.2.7 (Ronquist et al., 2012). Model selection for the ML analysis followed recommendations made in the RaxML user manual. One thousand rapid bootstraps were performed followed by a thorough ML search using a GTR substitution model and gamma distributed rate heterogeneity across a single partition. For the *rpb2* and *rpb1* datasets, both with fewer than 50 taxa, we modeled the data with a GTRGAMMA model across a single partition, again following recommendations in the RaxML user manual. For the BI analyses, we modeled the data according to jModelTest 2 0.1.11 under the AIC criterion (Guindon & Gascuel, 2003; Darriba et al., 2012) at the CIPRES Science Gateway (Miller et al., 2010). We then executed the nexus alignments in MrBayes for 1.5 million (*rpb1*), four million (*rpb2*), and ten million (rDNA) generations saving trees and other parameters every thousand generations followed by a 25% burn-in after inspection of convergence between two independent runs. A 50% majority-rule consensus tree was constructed and posterior probabilities (PP) calculated. Bootstraps >70% and PPs greater than 0.95 were considered as evidence of strong support for any given internode. The alignments (ITS+28S, *rpb2*, *rpb1*) and ML and BI tree files are available at inocybaceae.org and as Suppl. Material 1–3, respectively.

Results

Phylogeny

The following DNA substitution models were selected for the BI analyses: rDNA (TrN+I+G), *rpb2* (TrN+I), and *rpb1* (TrNef+G). Examination of the average standard deviation of split frequencies, estimated sample size (ESS), and potential scale reduction factors (PSRF) values showed the number of generations run in the BI analyses was sufficient for each of the three datasets. Both ML and BI produced similar topologies, thus, only ML topologies are shown including significant bootstrap values and PPs.

A total of 84 new sequences was produced for this study (28 of ITS, 22 of 28S, 16 of *rpb2*, and 18 of *rpb1*). The ITS sequence of collection LDG18697 (MT239042) from lowland *Quercus* forest in Costa Rica (Singer et al., 1983) clustered in the clade ultimately determined as *Inocybe velicopia* but was omitted from final phylogenetic analyses due to the presence of unusual autapomorphic positions.

TABLE 1. TAXON SAMPLING FOR PHYLOGENETIC ANALYSES INCLUDING SPECIMEN-VOUCHERS AND ENVIRONMENTAL SAMPLES, GEOGRAPHIC ORIGIN, PLANT HOST ASSOCIATION, AND GENBANK ACCESSION NUMBERS ANALYZED FOR THIS STUDY. NEW DNA SEQUENCES ARE HIGHLIGHTED IN BOLD

Species	Specimen-voucher or environmental sample	Geographic origin	Plant host associates	GenBank Accession Numbers			
				ITS	28S	*rpb2*	*rpb1*
Inocybe acriolens	ACAD11669	Nova Scotia	In ravine, *Tsuga*	MG489945	**ON113311**	–	–
	AU10493 (isotype)	Nova Scotia	*Picea-Abies*	KY923018	KY923038	–	–
	AWW270 (TENN)	Rhode Island	Mixed deciduous trees	**ON116974**	**ON113312**	MH577491	–
	JCS071005D (TENN)	Massachusetts	Not recorded	**ON116975**	MH577492	MH577492	**ON221361**
	LVK12311	Rhode Island	*Pinus*	**ON116976**	**ON113313**	**ON221345**	**ON221362**
	LVK14105	Maine	*Pinus*, *Quercus*	**ON116977**	**ON113314**	**ON221346**	**ON221363**
	LVK15086	Maine	*Pinus*, *Quercus*	**ON116978**	**ON113315**	**ON221347**	**ON221364**
	RAS869 (TENN)	New York	*Tsuga*, *Fagus*, *Pinus*	**ON116979**	–	–	–
I. albodiscoides	DAVFP 28147	British Columbia	*Pseudotsuga*	HQ650750	–	–	–
	JK189 (holotype TENN)	Washington	*Pseudotsuga*, *Arbutus*	**ON116980**	**ON113316**	**ON221348**	–
	KGP30	California	Coastal pine forest (*Pinus muricata*)	DQ822813	–	–	**ON217548**
	KGP96	California	Coastal pine forest (*P. muricata*)	–	–	–	**ON217549**
	PBM554	Washington	*Pseudotsuga*, *Tsuga*	**ON116981**	**ON113317**	–	–
	PBM1390	Washington	*Pseudotsuga*	–	EU307819	EU307821	EU307820
	RHM18–1	Washington	Conifers mixed with hardwoods	MH578011	–	–	**ON217550**
	TAM2010 (ECM root tip)	California	Mixed evergreen forest	AY310824	–	–	–
	UBC F18983	British Columbia	Not recorded	HQ604447	–	–	–
	UBC F19135	British Columbia	Not recorded	HQ604451	HQ604451	–	–
	UBC F23765	British Columbia	Not recorded	KC581308	KC581308	–	–
	UBC F28409	British Columbia	Not recorded	KP454033	KP454033	–	–
I. floridana	FLAS-F-60946	Florida	*Quercus*, *Carya*, *Pinus*	MH016905	MH620263	–	–
	PBM4529 (TENN)	Florida	*Quercus*, *Pinus*	**ON116982**	**ON113318**	–	–
I. grammata	21682	Italy	Not recorded	JF908264	–	–	–
	ACAD10539 (isotype of *I. permucida*)	Nova Scotia	Mixed hardwood-conifer forest	HQ201361	HQ201362	–	–
	AH15662	Spain	*Betula*, *Corylus*	MK480528	MK480522	–	–
	AH22127	Spain	*Betula*	MK480527	MK480521	–	–
	AH47717	France	*Picea*	MK480525	MK480519	–	–
	EL190–06	Sweden	Not recorded	KT958933	KT958933	–	–
	Olsen86	Sweden	Not recorded	KT958932	KT958932	–	–
	PBM2558 (TENN)	New Hampshire	*Tsuga*, *Betula*, *Picea*	**ON116983**	JQ313562	**ON221349**	**ON221365**

Table 1. Continued

Species	Specimen-voucher or environmental sample	Geographic origin	Plant host associates	GenBank Accession Numbers			
				ITS	28S	*rpb2*	*rpb1*
	PBM2602 (TENN)	Tennessee	*Betula*, *Picea*	**ON116984**	JN974977	**ON221350**	–
	PBM4210 (TENN)	North Carolina	*Abies*	MT237495	–	–	–
	PBM4272 (TENN)	North Carolina	*Abies*	MT196989	**ON113319**	–	**ON221366**
I. grammatoides	A15-17B root tip	Quebec	*Populus*	EU554696	–	–	–
	ACAD11762	Nova Scotia	*Betula*, *Fagus*, *Acer*, *Populus tremuloides*	MH024870 MH024858	MH024881	–	–
	AH46618 (holotype)	Spain	*Quercus*	MK480531	MK480524	–	–
	F195A ECM	Wisconsin	*Populus tremuloides*	JX316792	–	–	–
	Contig_20	Quebec	*Populus* rhizosphere	FJ626938	–	–	–
	HB33	China	*Pinus*	MH366755	–	–	–
	HQ72	China	*Pinus*	MK342063	–	–	–
	KR-M-0044740	Germany	Not recorded	MT006018	–	–	–
	KR-M-0044790	Germany	Not recorded	MT005870	–	–	–
	KR-M-0044811	Germany	Not recorded	MT005891	–	–	–
	KR-M-0044823	Germany	Not recorded	MT005896	–	–	–
	LN-303 (ECM *Pinus*?)	China: Liaoning	*Pinus*?	LC622582	–	–	–
	LVK21232	Maine	*Quercus*, *Pinus*	**ON478235**	–	**ON246331**	**ON221377**
	LVK21312	New York	*Abies*, *Picea*, *Populus*, *Betula*	**ON116985**	**ON113320**	**ON221351**	**ON221367**
	LVK21459	Pennsylvania	*Picea* and mixed woods	**ON116986**	**ON113321**	**ON221352**	**ON221368**
	T50_11 root tip	Quebec	*Populus*	EU554739	–	–	–
I. panamica	AC59 (holotype UCH)	Panama	*Quercus*, *Oreomunnea*	**ON116987**	**ON113322**	**ON221353**	–
	AC98 (ARIZ)	Panama	*Quercus*, *Oreomunnea*	**ON116988**	**ON113323**	–	–
	AC265 (ARIZ)	Panama	*Quercus*, *Oreomunnea*	**ON116989**	**ON113324**	**ON221354**	–
	REH7181 (NY)	Costa Rica	*Quercus*	**ON116990**	JN974980	–	–
I. panamica cf.	REH7995	Costa Rica	*Quercus*	**ON116991**	JN974978	**ON221355**	–
I. sindonia	JV5054 (WTU)	Finland	*Populus*, *Betula*, *Picea*	**ON116992**	KC305362	KC305416	**ON221369**
	PBM2048 (WTU)	Washington	*Picea*	–	–	AY337401	AF390019
	PDD80239	New Zealand	*Pinus*	KP636833	KC305363	–	–
I. soluta	JV7811F (WTU)	Finland	*Pinus*	**ON116993**	JN974987	–	**ON221370**
I. stellatospora	PBM963 (WTU)	Washington	*Pseudotsuga*, *Tsuga*	–	–	AY337403	–
	PBM4619 (TENN)	New York	*Abies*, *Picea*, *Betula*, *Pinus*	**ON116994**	**ON113325**	**ON221356**	–
I. velicopia	ACD0106	Wisconsin	Not recorded	MW464406	–	–	–
	H1C_2_11 root tip	New York	*Castanea*	JX030222	–	–	–
	H2Wb_3 root tip	New York	*Castanea*	JX030229	–	–	–
	H4Ls_1X roo tip	New York	*Castanea*	JX030233	–	–	–
	iNat 29,219,095	New York	*Quercus*, *Fagus*	MZ226438	–	–	–
	iNat 56,982,160	Indiana	Not recorded	OM473867	–	–	–
	LDG18697	Costa Rica	*Quercus*	MT239042	–	–	–
	LVK12095	New Jersey	Not recorded	**ON116995**	**ON113326**	**ON221357**	**ON221371**
	LVK13259	New York	*Quercus*	**ON116996**	**ON113327**	**ON221358**	**ON221372**
	LVK14164	New York	*Quercus*	**ON116997**	**ON113328**	–	**ON221373**

TABLE 1. CONTINUED

Species	Specimen-voucher or environmental sample	Geographic origin	Plant host associates	GenBank Accession Numbers			
				ITS	28S	*rpb2*	*rpb1*
	LVK18101	New York	*Quercus*	–	**ON113329**	**ON221359**	**ON221374**
	LVK18412X	New Jersey	Mixed woods	**ON116998**	**ON113330**	**ON221360**	**ON221375**
	PBM2826	New York	*Quercus*, *Carya*, *Fagus*	**ON116999**	**ON113331**	–	–
	PBM3336 (holotype TENN)	Tennessee	*Quercus*	**ON117000**	JN974979	MH577493	–
	PRL5420	Indiana	*Quercus* dominated woodland	GQ166895	–	–	–
	RA607–1	Arkansas	Not recorded	MK217440	–	–	–
	REH8024	Costa Rica	*Quercus*	**ON117001**	**ON113332**	MH577463	**ON221376**
	SDR5925	Indiana	Not recorded	OM473364	–	–	–
	SDR9676	Indiana	Not recorded	OM473588	–	–	–
I. vestalis	STU-F-0901263 (holotype)	Germany	*Picea*, *Abies*, *Fagus*	MN512328	MN512328	–	–

Three different gene trees are presented – the rDNA tree (including 76 tips and 2168 sites) based on analysis of combined ITS+28S (Fig. 1), the *rpb2* gene tree (including 26 tips and 776 sites) (Fig. 2), and the *rpb1* gene tree (including 25 tips and 1450 sites) (Fig. 3). The rDNA gene tree recovered eight species in the *Inocybe grammata* group, described formally below as *I.* sect. *Albodiscae*. The samples for most of these eight species included sequences of their types: *I. grammatoides* (type), *I. acriolens* (type), *Iais floridana*, *I. grammata* (syns. *I. albodisca*, *I. permucida* (type pro parte)), *I. albodiscoides* sp. nov. (type), *I. panamica* sp. nov. (type), *I. velicopia* sp. nov. (type), and *I. vestalis* (type). All species represented in this tree by more than one sample (*I. vestalis* notwithstanding) received strong support as monophyletic species-level lineages. At least two sequences could not be placed with confidence: a sample identified as *I. acriolens* from China and a sample similar to *I. panamica* from Costa Rica. Within *I.* sect. *Albodiscae*, *I. vestalis* was strongly supported as sister to the rest of the section, within which *I. velicopia* was strongly supported as sister to the remaining species. *Inocybe vestalis*, a conifer associate described recently from Germany, lacks a bicolorous pileus but shares several features in common with *I.* sect. *Albodiscae*, viz., the presence of superficial fibrils on the margin of the pileus and similar stipe and micro morphology (Bandini et al., 2020). In addition, the strongly supported sister pair *I. acriolens* and *I. grammatoides* was also recovered.

Six species were included in the *rpb2* gene tree (Fig. 2). *Inocybe* sect. *Albodiscae* was strongly supported as a monophyletic group with respect to the outgroups, and five of the six species sampled formed significantly supported monophyletic species-level lineages. Data from *rpb2* also supported a strong sister group relationship between *I. acriolens* and *I. grammatoides* as in the rDNA analyses above. However, several samples of *I. velicopia* formed a weakly supported paraphyletic grade from which the remaining lineages emerged.

The *rpb1* gene tree included five species (Fig. 3), each one receiving strong support and distinction as distinct species-level lineages (*Inocybe albodiscoides*, *I. acriolens*, *I. grammata*, *I. grammatoides*, *I. velicopia*). *Inocybe* sect. *Albodiscae* also received strong support as a monophyletic group, however, four samples from *I. albodiscoides* clustered with strong support with an outgroup, *I. sindonia*. One of these four samples (RHM18–1) is a *rpb1* pseudogene based on frame-shift mutations in exon regions. Indeed, it was the only sample of the four sequences sequenced upstream of the intron2 region. However, given the monophyletic nature of all *rpb1 albodiscoides* samples, it is reasonable to conclude they all represent pseudogenes and paralogues. No *rpb1* orthologues from *I. albodiscoides* were recovered. Like the rDNA

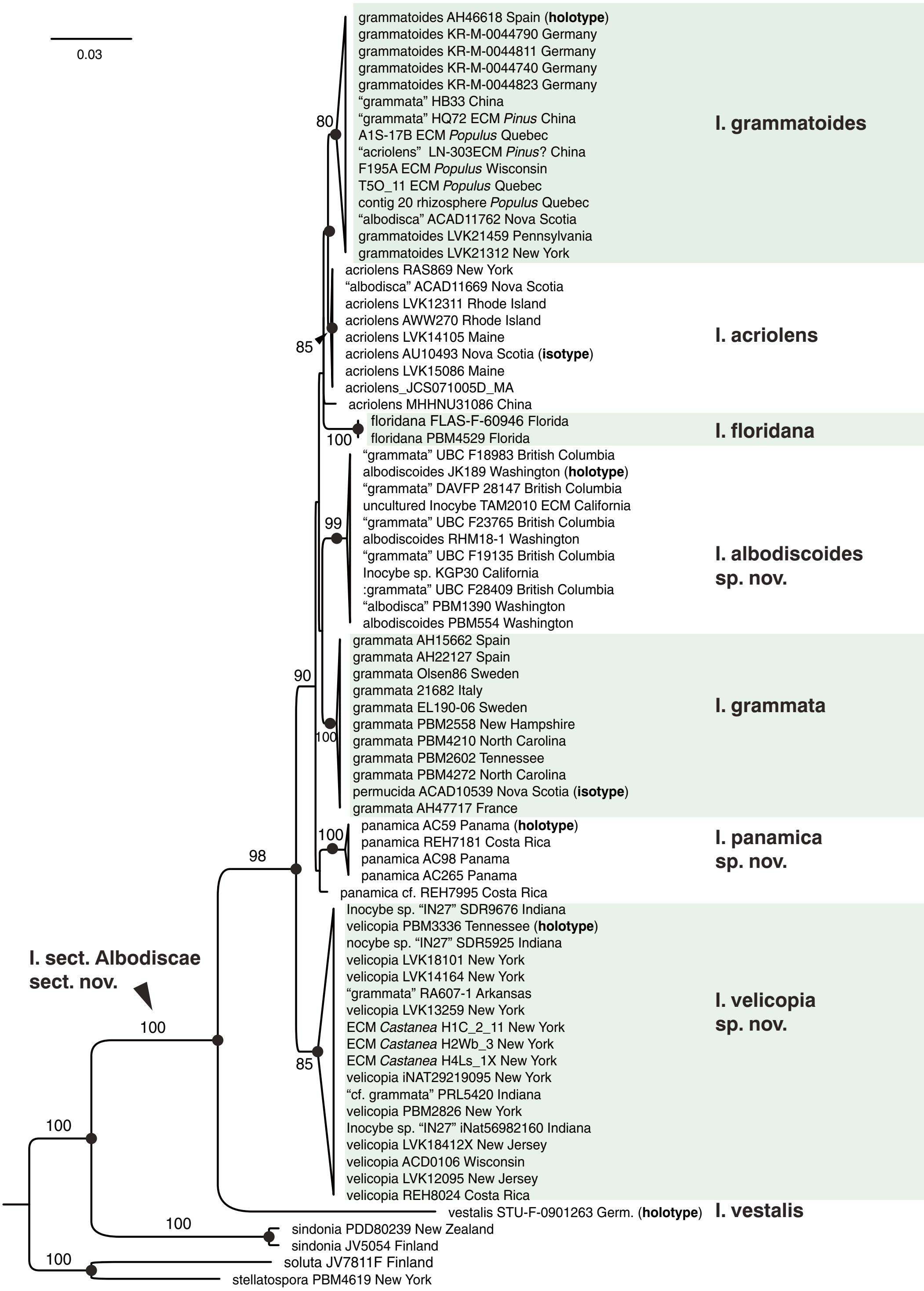

Fig. 1. Phylogeny of the *Inocybe grammata* group (*I.* sect. *Albodiscae*) inferred from ML analysis of concatenated ITS and 28S data. Numbers above or near internodes and branches are bootstrap values (only those >70% are shown). Black filled circles indicate nodes with >0.95 PP. *Inocybe stellatospora* and *I. soluta* were used to root the tree.

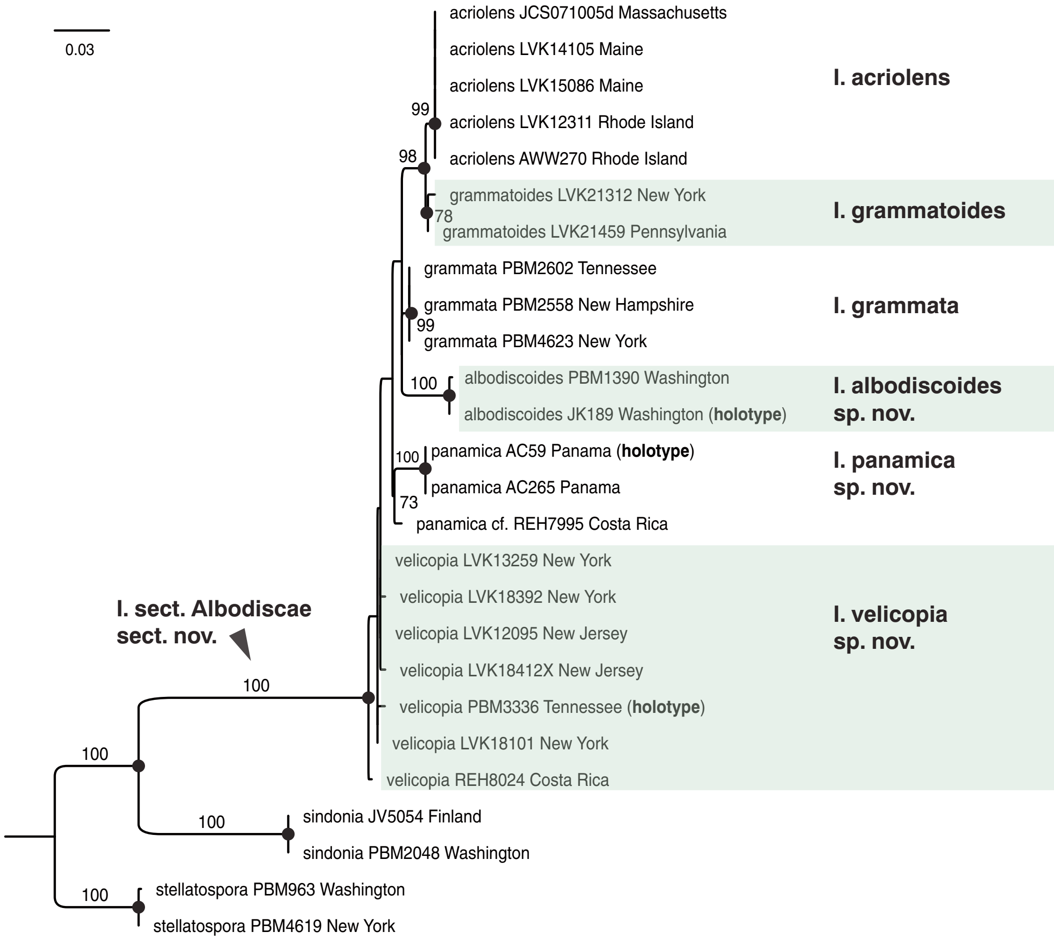

Fig. 2. Phylogeny of the *Inocybe grammata* group (*I.* sect. *Albodiscae*) inferred from ML analysis of *rpb2* data. Numbers above or near internodes and branches are bootstrap values (only those >80% are shown). Black filled circles indicate nodes with >0.95 PP. *Inocybe stellatospora* was used to root the tree.

and *rpb2* results, both *I. acriolens* and *I. grammatoides* were recovered as a strongly supported species pair. However, unlike the rDNA and *rpb2* results, *I. grammata* occupied a strongly supported position sister to the remaining lineages in contrast to *I. velicopia*. Notably, *rpb1* amplicons of *I. grammata* were smaller than other samples due to the truncation of *rpb1*-intron2, which was 136 bp in length. By contrast, *rpb1*-intron2 ranged between 521 and 526 bp in size for *I. velicopia*, *I. acriolens*, and *I. grammatoides*, and 429 bp in the pseudogene sequence of *I. albodiscoides*. Typically, *rpb1*-intron2 is 510—550 bp in length across the Inocybaceae (Matheny, 2005). Lastly, samples of *I. velicopia* were reciprocally monophyletic in the rDNA and *rpb1* gene trees but not in the *rpb2* gene tree.

Taxonomic Treatment

Inocybe sect. ***Albodiscae*** Matheny, **sect. nov.**—Type: *Inocybe grammata* Quél. MycoBank MB843514.

Diagnosis.—Pileus often bicolorous due to the presence of a pronounced white or pale velipellis over the disc, some species with persistent pallid superficial fibrils especially over the margin; most species with an entirely pruinose and white to pinkish tinged stipe often with a marginate or swollen basal bulb (but this sometimes not distinct), angular to angular-nodulose pigmented basidiospores with mean spore lengths <10 μm, and thick-walled cheilo-, pleuro-, and caulocystidia. Odor often distinctive – spermatic, unpleasant, of green corn, or sweetly aromatic. Forming a monophyletic group based on analysis of multiple genetic loci. North temperate and neotropical in distribution and forming plant associations with Fagales,

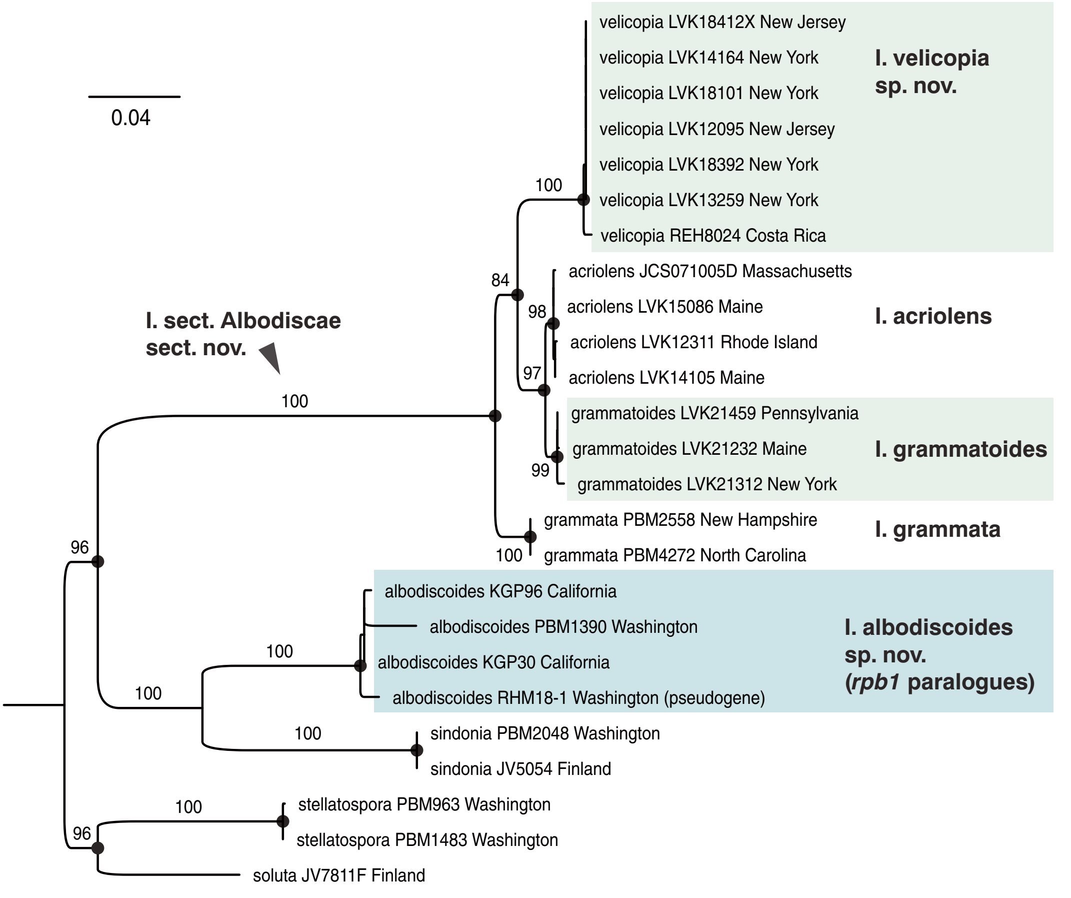

FIG. 3. Phylogeny of the *Inocybe grammata* group (*I.* sect. *Albodiscae*) inferred from ML analysis of *rpb1* data. Numbers above or near internodes and branches are bootstrap values (only those >80% are shown). Black filled circles indicate nodes with >0.95 PP. *Inocybe stellatospora* and *I. soluta* were used to root the tree.

Salicaceae, and Pinaceae. Muscarine absent or in very low concentration in *I. grammata* and *I. albodiscoides*.

Included species.—*Inocybe acriolens*, *I. albodiscoides*, *I. floridana*, *I. grammata*, *I. grammatoides*, *I. panamica*, *I. velicopia*, *I. vestalis.*

Species of uncertain position.—*Inocybe pargasensis*, *I. entolomatospora.*

Notes.—Included species in the section have been confirmed by molecular phylogenetic analysis. The section is cleaved from *Inocybe* sect. *Marginatae*, which is not monophyletic as currently circumscribed. The type of *I.* sect. *Marginatae* is *Inocybe asterospora*, which, along with most or all species of the section, is characterized by stellate basidiospores. Species of *I.* sect. *Rubellae* Kühner & Bousier are distinguished from those in *I.* sect. *Albodiscae* by reddening flesh. Species of *I.* sect. *Calosporae* J.E.Lange are characterized by spinose spores (see Singer, 1986 for characterization of these three sections). Species of the *I. xanthomelas* group or "xanthomelas clade" differ either by their darkening stipe and/or elongate or slender and nearly lageniform cystidia characterized by a protruding neck (Esteve-Raventós et al., 2015, 2016). Species of the *I. praetervisa* group (*I.* subsect. *Praetervisae* Bon), which are distantly related to the *I. xanthomelas* group, differ by the stipe color without pinkish or reddish tinges and sparse to absent caulocystidia on the lower part of the stipe (Esteve-Raventós et al., 2016; Larsson et al., 2017). Species of the *I. mixtilis* group are isolated phylogenetically and lack the conspicuous pallid pileal disc and flushes of color to the stipe.

Members of *I.* subsect. *Oblectabiles* Bon are characterized by the stipe that is pinkish or nearly concolorous with the pileus; indeed, Bon (1998) classified species here in *I.* sect. *Albodiscae* within his subsect. *Oblectabiles*. However, this subsection is not monophyletic and instead seems to be centered around species without a heavy velum on the pileus such as *I. oblectabilis* (Britzelm.) Sacc., *Inodrillia nucleata* Murrill, *I. nobilis* (R.Heim) Alessio, *I. pallida* Velen., *Idris dunensis* P.D.Orton, and *I. tiliae* Franchi, M.Marchetti & Papetti.

Two studies reported the absence of muscarine from *Inocybe albodiscoides* (Brown et al., 1962 as *I. albodisca*; Robbers et al., 1964 as *I. albodisca*) and *I. grammata* (Kosentka et al., 2013). One study reported very low muscarinic activity in *I. albodiscoides* (Malone et al., 1962 as *I. albodisca*).

Inocybe acriolens Grund & D.E.Stuntz, Mycologia 67: 19 (1975).—Type: Canada, Nova Scotia: Scott's Bay, Kings Co., singly in *Picea-Abies* woods, 19 Aug 1973, *K. A. Harrison AU10493* (holotype: ACAD [n.v]; isotype: WTU [!]). (Figs. 4, 10A–B.)

Pileus 20–25 mm wide, broadly convex-expanded, umbonate, margin broadly rounded; surface dry, unbroken at the center; margin appressed silky fibrillose and slightly rimose, forming tiny furfuraceous appressed scales, everywhere overlain by a persistent superficial layer; cream to pale brownish gray (4C3) on the umbo, umbrinous (Tawny-Olive, 5D5) between the umbo and margin but flushed with reddish orange or pinkish tints, grayish brown (Sepia) beneath the superficial fibrils on the margin, at times the margin distinctly pallid due to the dense accumulation of superficial fibrils there; flesh 1–2 mm thick, pallid, soft, unchanging upon exposure; odor penetrating, unpleasant, complex, a mixture of green corn and strong pungent-aromatic (not sweet or fragrant) components. Lamellae narrowly adnate, moderately close to subdistant with several tiers of lamellulae, ventricose, broad (3–4 mm deep); light brown (Avellaneous), becoming brown (5E6); edges indistinctly pallid-fimbriate to concolorous. Stipe 40–45 × 4–5 mm, terete, equal or with slight marginate bulb; surface dry, satiny, pruinose the entire length; apex flushed with pink, elsewhere brown or umbrinous (5D5) but with a reddish tinge; solid, flesh pallid brownish.

Basidiospores 6.5–*7.8*–9 × 5–*5.7*–6.5 μm, Q 1.17–*1.37*–1.58 (n=36/2), oblong, polyhedral, or angular in outline, often with the apex narrowed to a blunt point, with 6–10 low blunt nodules, at times merely angular. Basidia 26–33 × 8–10 μm, 4-sterigmate, clavate, hyaline. Pleurocystidia 45–60 × 11–21 μm, fusiform or widest below or above the middle; thick-walled, walls 3.5–5.5 μm thick, dull yellow; apices obtuse, crystalliferous. Cheilocystidia similar to pleurocystidia, mixed with paracystidia and occasional basidia. Caulocystidia similar to hymenial cystidia, mixed with cauloparacystidia, descending entire length of stipe. Pileipellis a cutis of brown-walled hyphae 4–12 μm wide, overlain by interwoven superficial hyphae, these hyaline and 3–7 μm wide. Clamp connections present.

Distribution and habitat.—Solitary, scattered or gregarious, singly, on acid soil in *Tsuga canadensis* forest mixed with *Fagus* and *Pinus*, in mixed hardwood forest, and under pines (type reported in *Picea-Abies* forest), southeast Canada (Nova Scotia, type), New England (Rhode Island, Massachusetts), and New York.

Phenology.—June to November.

Etymology.—Named *acriolens* by Grund and Stuntz (1975) in reference to the pungent smell of the basidiomata.

Additional specimens examined.—**CANADA. Nova Scotia**: Kentville, Agricultural Experimental Station, in ravine (*T. canadensis*), 17 Aug 1976, *D. E. Stuntz* (ACAD11669 as "*I. albodisca*").

UNITED STATES. Maine: York Co., Alewife Woods, Kennebunk, on soil in mixed woods under mostly *Pinus*, *Quercus*, 14 Jul 2014, *L. V. Kudzma LVK14105* (pers. herb.); ibid., 20 Jul 2015, *L. V. Kudzma LVK15086* (pers. herb.). **Massachusetts**: Worcester Co., Grafton, on sol, 10 Nov 2009, *J. C. Slot JCS071005D* (TENN-F-063922). **New York**: Essex Co., Henry's Woods Loop Trail, gregarious on acid soil in mixed woods under *Tsuga*, *Fagus*, *Pinus*, 10 Aug 2021, *R. A. Swenie RAS869* (TENN-F-076508). **Rhode Island**: Providence Co., Lincoln Woods State Park, on soil under mixed deciduous trees, 28 Jun 2006, *A. W. Wilson AWW270* (TENN-F-063963); Washington Co., Exeter, Arcadia Wildlife Management Area, Brookie Trail, on soil under *Pinus*, 8 Oct 2012, *L. V. Kudzma LVK12311* (pers. herb.).

Notes.—The morphological description is modified from Grund and Stuntz (1975) and supplemented by observations from collections made in the field and from molecularly annotated herbarium specimens. *Inocybe acriolens* was

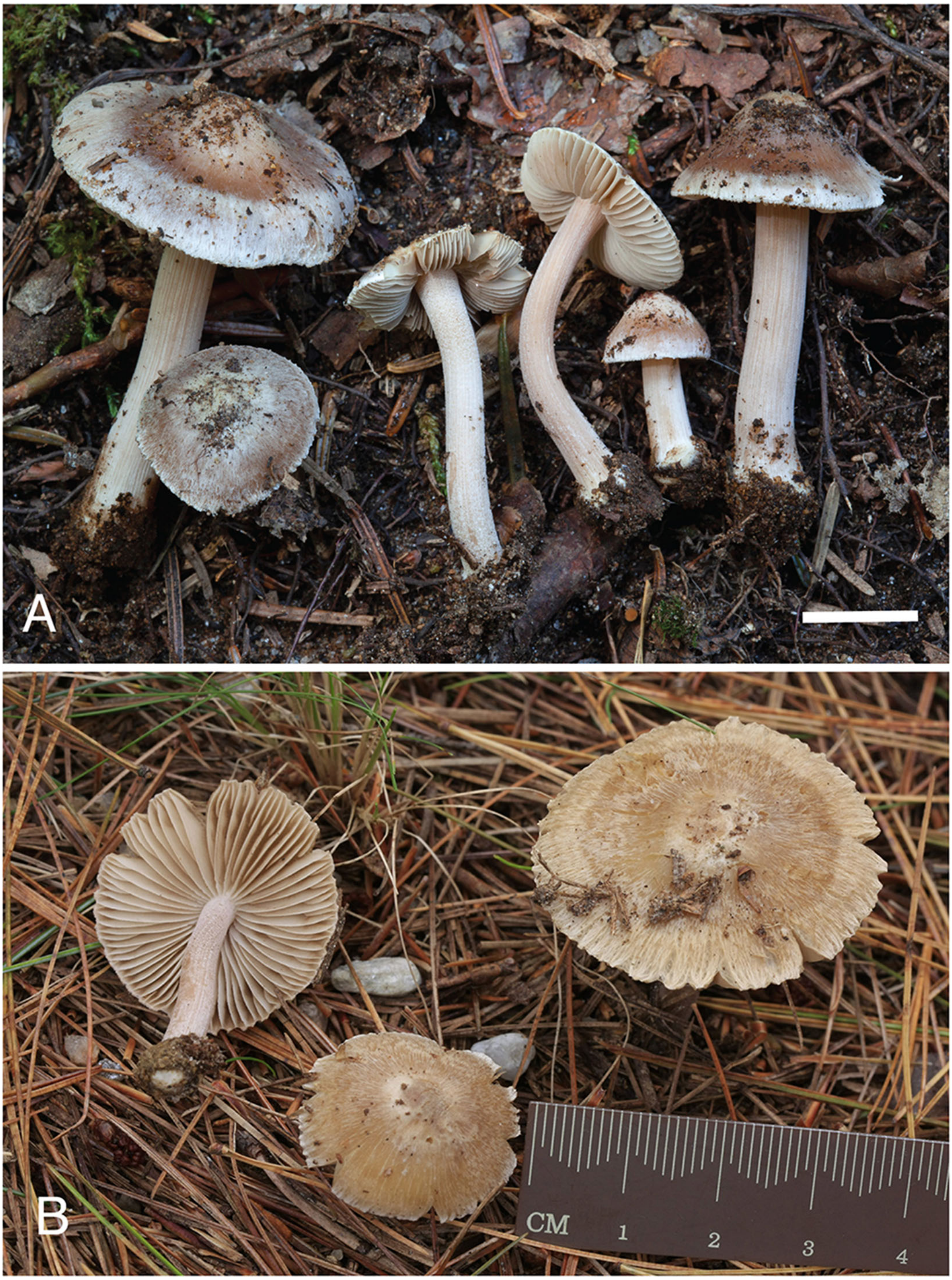

Fig. 4. *Inocybe acriolens*. **A.** Basidiomes of *RAS869* (TENN-F-076508) from New York (photo by R.A Swenie). **B.** Basidiomes of *LVK12311* (Kudzma, pers. herb.) from Rhode Island (photo by L.V. Kudzma). Scale bars = 1 cm.

originally described from a single collection in Nova Scotia under spruce-fir and characterized by the zonate coloration, pallid persistent superficial layer, the pungent disagreeable odor, and equal non-bulbous stipe. Fortunately, we successfully sequenced the ITS and a portion of the 28S from the type (AU10493) and have come to a better understanding of the morphological and ecological amplitude of this species. First, none of our sequenced collections originated in spruce-fir forest; rather these were made in mixed hemlock forest, mixed hardwood forests, and pine forests. Later, Grund and Stuntz (1980) documented *I. albodisca* from Nova Scotia, however, the two collections cited in that study (and sequenced here) represent *I. acriolens* (ACAD11669 from hemlock forest) and *I. grammatoides* (ACAD11762 in beech-maple forest under birch and aspen). Based on these assorted collections, *I. acriolens* may be a hemlock and pine associate though we cannot exclude the possibility of association with beech as well. Collections we originally referred to as *I. acriolens* made under spruce-fir exclusively have been re-determined as *I. grammata* after molecular annotation. Taken together, the reference to spruce-fir in the protologue of *I. acriolens* raises questions about its accuracy. Also, in contrast to the protologue (again based on a single collection), the stipe at times does feature an indistinct marginate bulb. The pileus color may also vary depending on the thickness of the extensive superficial layer of fibrils, especially at the margin, ranging from a warm reddish brown to yellowish brown or umbrinous (Tawny-Olive) as shown in photographs here (Fig. 4). Yellowish brown forms of *I. acriolens* could be confused with *I. velicopia*, but the latter occurs under oak and has a smooth margin free of the distinct superficial fibrils that appear to be characteristic of *I. acriolens*.

Considering our observations above, *Inocybe grammata* is best distinguished from *I. acriolens* by occurrence in spruce-fir forests or association with fir and birch. *Inocybe albodiscoides*, described below, differs from *I. acriolens* by the larger basidiomes, smaller basidiospores, and occurrence with Douglas fir and Western hemlock in the Pacific Northwest.

Inocybe albodiscoides Matheny, **sp. nov.—**Type: USA, Washington: Jefferson Co., Port Townsend, Cappy's Trails, 48.1312° lat., −12.7898° long., on acid soil under *Pseudotsuga menziesii*, *Arbutus menziesii*, and *Thuja plicata*, 30 Nov 2021, *J. Kalichman JK189* (holotype: TENN-F-076659 [!]). MycoBank MB843511. GenBank ITS = ON116980. (Figs. 5, 10C–D.)

Diagnosis.—Most similar to *Inocybe grammata* (=*I. albodisca*) but differs from it by the larger and more robust basidiomes, smaller basidiospores, occurrence in the Pacific Northwest, and unique phylogenetic position.

Pileus 30–60 mm wide, conical to campanulate or plano-convex, at last plane with arched margins, margin decurved to straight; surface greasy-moist and smooth over the disc, fibrillose to fibrillose-scaly or with a furfuraceous appearance around the center and towards the margin, the small scales becoming more acute with loss of moisture; noticeably bicolorous (less often tricolorous) due to the whitish or pallid disc contrasting with the pinkish gray to grayish brown margin (7.5YR 6/2–5/2; Vinaceous-Buff, Avellaneous, or Wood Brown), KOH negative; flesh firm, white, unchanging upon exposure, PDAB negative; odor spermatic at least when first cut, unpleasant or similar to green corn, or not remarkable. Lamellae sinuate to adnexed, close with several tiers of lamellulae; light gray at first, becoming pale brown (10YR 6/3) for long durations, at last brown (10YR 5/3), ventricose, broad, up to 5 mm deep. Stipe 45–65(100) × 4–7(15) mm, terete to compressed, usually with a distinct marginate bulb 8–14 mm wide (bulb occasionally not so distinctive); surface dry, pruinose the entire length and with a satiny appearance; whitish or pallid, at times with a pale yellow (2.5Y 7/4), pale ochraceous buff, or very pale brown (10YR 7/4; Fawn Color to Vinaceous Buff) undertone, or with a pale pinkish flush (incarnate) at the apex; flesh white or pallid throughout, at times with a flush of pink or more rosy-ochraceous at the apex, solid.

Basidiospores 5–*6*–6.5(7.5) × (4)4.5–*4.8*–5.5 μm (n=36/3), Q (1.00)1.10–*1.28*–1.40(1.63), angular with few (1–6) or almost no nodules, light yellowish brown (Ochraceous-Buff) with slightly thickened walls. Basidia 22–27 × 8–9 μm, 4-sterigmate, clavate, hyaline. Pleurocystidia 48–69 × 14–20 μm, fusiform, fusiform-ventricose, or obclavate, necks short or at least not long; thick-walled, walls 1.5–2.5 μm; apices obtuse, crystalliferous.

Fig. 5. *Inocybe albodiscoides*. **A.** Basidiomes of *N. Siegel s.n.* from California (photo by N. Siegel). **B.** Basidiomes of *JK189* (holotype TENN-F-076659) from Washington (photo by J. Kalichman). Scale bars = 1 cm.

Cheilocystidia similar to pleurocystidia and mixed with thin-walled hyaline paracystidia. Caulocystidia similar to hymenial cystidia but at times longer and cylindric (50–99 × 11–15 µm), slightly thick-walled or thin-walled, mixed with cauloparacystidia and descending entire length of stipe. Pileipellis a cutis composed of smooth and incrusted hyphae 2–10 µm wide, pale yellowish brown in mass. Clamp connections present.

Distribution and ecology.—Gregarious to scattered singly on acid soil under conifers, namely associated with *P. menziesii* and/or *Tsuga* in the Pacific Northwest (British Columbia to Oregon), also with *Pinus* in northern California, at low elevations.

Phenology.—October to January in the Pacific Norwest and through February in California.

Etymology.—Named *albodiscoides* (L.), referring to prior reference of this species as *Inocybe albodisca* Peck.

Additional specimens examined.—**UNITED STATES. California**: Marin Co., Point Reyes National Seashore, on soil in coastal pine forest with *Pinus muricata*, no date, *K. G. Peay KGP30* (UC); ibid., *K. G. Peay KBP96* (UC). **Oregon**: Linn Co., H.J. Andrews Experimental Forest, on soil under conifers, 23 Oct 1999, *P. B. Matheny PBM1748* (WTU-F-037909). **Washington**: Island Co., Camano Island State Park, on soil under *Pseudotsuga*, 4 Nov 1999, *P. B. Matheny PBM1770* (WTU-F-037908); King Co., Seattle, University of Washington campus, on soil under *Pseudotsuga*, 3 Dec 1998, *P. B. Matheny PBM1390* (WTU-F-037918); King Co., Seattle, University of Washington campus, east of Bloedel Hall, gregarious to scattered singly on acid soil under *P. menziesii*, 12 Nov 1999, *P. B. Matheny PBM1803* (WTU); King Co., Pine Lake State Park, 5 Nov 2000, *P. B. Matheny PBM2040* (WTU); Kitsap Co., Seabeck, on soil under *Pseudotsuga*, *Tsuga*, 28 Jun 1997, *P. B. Matheny PBM554* (WTU); ibid., 11 Jul 1997, *P. B. Matheny PBM576* (WTU-F-037915); ibid., 25 Oct 1997, *P. B. Matheny PBM798* (WTU-F-037916); ibid., 25 Oct. 1997, *P. B. Matheny PBM806* (WTU); ibid., 21 Nov. 1998, *P. B. Matheny PBM1365* (WTU-F-037917); Pierce Co., Tacoma, Beckonridge Development, in lawn under *Pseudotsuga*, 21 Jan 2013, *S. A. Trudell SAT1302102* (TENN-F-074028); Snohomish Co., Point Wells, in sandy soil along a road through a hemlock stand, 18 Oct 1935, *D. E. Stuntz Stz379* (WTU); Whatcom Co., Stimpson Family Nature Reserve, on soil along path under conifers mixed with hardwoods, 14 Jan 2018, *R. H. Morrison RHM18–1* (TENN-F-073746).

Notes.—Prior workers (Stuntz, 1947) and authors of field guides (e.g., Lincoff, 1981; Desjardin et al., 2015) employed a broad concept of *Inocybe albodisca* and for *I. grammata* (Vauras, 1997), in which large robust specimens from the Pacific Northwest were included. However, phylogenetic analyses (Figs. 1, 2, 3), micromorphology (Fig. 9), and ecology strongly support the distinction of Pacific Northwest specimens as a separate species described here as *I. albodiscoides*. The spores of *I. albodiscoides* are noticeably smaller than any other species in *I.* sect. *Albodiscae* ranging mostly from 5 to 6.5 × 4.5–5.5 µm in size and typically featuring an angular appearance with (very) few nodules. *Inocybe grammata* is similar to *I. albodiscoides* but differs generally by the often smaller basidiomes, larger spores, occurrence in in eastern North America (and Europe) under spruce, fir, and birch, and unique phylogenetic position across multiple loci. Many rDNA sequences of materials from the Pacific Northwest, especially from British Columbia, are currently labeled *I. grammata* in GenBank, but these should be re-annotated as *I. albodiscoides* (Fig. 1, Table 1). Basidiomes of *I. panamica* (described below) can reach a similar large size as *I. albodiscoides*, but the former can be distinguished from the latter by the generally tan pileus coloration, larger spores, and occurrence in Central America under oak and *Oreomunnea mexicana* (Juglandaceae). *Inocybe velicopia* (also described below) occurs in the eastern United States and Costa Rica and is colored like *I. panamica*; it occurs under oak and chestnut.

Inocybe floridana Murrill, Quart. J. Flor. Acad. Sci. 8: 186 (1945).—Type: USA, Florida: Alachua Co., Gainesville, on shaded lawn, 25 Oct 1938, *W. A. Murrill F 19961* (holotype: FLAS-F-19961 [!]). (Figs. 6A, 10E–F.)

Pileus 17–35 mm wide, obtusely conical, expanding with raised margins in age, umbo absent, margin decurved; surface dry with thin whitish velipellis over the disc, at times with fine silky fibrils extending towards the pale yellow (2.5Y 8/4–7/4) to yellowish brown margin; smooth at the center and towards the margin or with a finely rimulose margin; flesh up to 5 mm thick under the disc, unchanging where cut or bruised, odor of green corn or somewhat fishy. Lamellae sinuate, moderately close, broad, ventricose, clay brown to yellowish brown, edges pallid and indistinctly fimbriate. Stipe 35–55 × 3–7 mm at the apex, terete, base rounded bulbous or indistinctly marginate and up to 10 mm wide; surface dry, densely pruinose down to the bulb, finely striatulate or satiny in appearance; off-white,

Fig. 6. *Inocybe floridana* and *I. grammata*. **A.** Basidiomes of *I. floridana PBM4529* from Florida (TENN-F-075552). **B.** Basidiomes of *I. grammata PBM4447* (TENN-F-075319) from North Carolina. Scale bars = 1 cm.

pallid, or tinged ivory, at times with a blush of pink at the apex; solid, flesh white.

Basidiospores (7.5)8.5–*9.3*–11.5(14) × (4)5–*5.5*–6(7) µm, Q(1.30)1.40–*1.71*–2.03(2.25) (n=34/2), irregularly angular or oblong-angular, trapeziform, or minimally angular, at times with a ventral depression, with few or 5–6 nodules or corners, apices usually conical, brownish yellow, with a slightly thickened wall and small but distinct apiculus. Basidia 27–42 × 7–9 µm, 2-, 4-sterigmate, clavate, hyaline. Pleurocystidia 44–78 × 13–20 µm, ventricose, fusiform, to utriform, often with a slender basal pedicel; very thick-walled, walls 3.5–5 µm thick, pale yellow to yellow; apices obtuse, crystalliferous. Cheilocystidia similar to pleurocystidia. Caulocystidia similar to hymenial cystidia, at times long-cylindric, descending entire length of stipe, mixed with cauloparacystidia. Pileipellis a cutis of repent, narrow, cylindric hyphae, these mostly smooth, occasionally some hyphae with faint incrustations, hyaline or very pale overall in mass, most hyphae 3–11 µm wide. Clamp connections present.

Distribution and ecology.—Scattered singly on calcareous sandy soil in mixed forests of *Quercus*, *Carya*, *Pinus*, also in lawns and high hammocks, northern Florida (holotype).

Phenology.—June to December.

Etymology.—Named *floridana* in reference to the geographic location.

Additional specimens examined.—**UNITED STATES. Florida**: Alachua Co., Gainesville, on ground in a high hammock, 21 Sep 1938, *W. A. Murrill F17460* (FLAS-F-17460); Putnam Co., Ordway-Swisher Biological Station by Timmons Creek bridge, on calcareous soil in *Quercus*-*Carya* dominated forest with *Pinus* also present, 20 Jun 2017, *M. E. Smith* et al. (FLAS-F-60946); ibid., south of Goose Lake, on calcareous sandy soil at side of road under *Quercus virginiana* and other *Quercus* spp. and *Pinus* including *P. elliottii*, 12 Dec 2020, *R. A. Swenie PBM4529* (TENN-F-075552).

Notes.—*Inocybe floridana* is distinguished from other species in *I.* sect. *Albodiscae* by the long and mainly angular basidiospores with few nodules or corners. The species has not been reported since Murrill (1945) described it as new from Gainesville, Florida. Both macro- and micromorphological features of more recently collected materials from northern Florida are consistent with the holotype, other than the entirely darkened grayish stipe of the single holotype specimen. However, supporting material cited by Murrill (1945) collected the previous month than the type does not feature a discolored stipe, nor do the modern materials examined here. Moreover, the protologue does not indicate any change of color to the stipe, thus we cannot exclude the possibility the stipe of the holotype collection became discolored due to improper preservation.

Attempts to direct sequence Murrill's types of *Inocybe* have not been successful due to apparent DNA degradation and contamination.

Inocybe grammata Quél, Bull. Soc. Amis Sci. Nat. Rouen, Sér. II 15: 162 (1880 [1879]).—Lectotype, designated by Vauras (1997: 37): Plate 2, Fig. 8 in Quélet, Bull. Soc. Amis Sci. Nat. Rouen, Sér. II. (1879) [n.v.]. (Figs. 6B, 10G–H.)

Inocybe albodisca Peck, Ann. Rep. N.Y. St. Mus. 51: 290. 1898.—Lectotype, designated by Vauras (1997: 37): USA, New York: Essex Co., North Elba [without precise locality], Aug [without day and year], *C. H. Peck s.n.* (NYSf159 [image!]).

Inocybe permucida Grund & Stuntz pro parte, Mycologia 75: 264 (1983).—Type: Canada, Nova Scotia: Kings Co., Bay of Fundy, Black Hole, 30 Aug 1973, *D. Grund 10,539* (holotype: ACAD-10539F [n.v.]; isotype: WTU-F-063182 [!]). GenBank ITS = HQ201361.

Inocybe grammata var. *chamesalicis* Bon & E.Ferrari, Boll. Gruppo Micol. 'G. Bresadola' (Trento) 45: 16 (2002).—Type: Italy, Val d'Olen, Foric Pass (Alagna Valsesia, VC), near *Salix herbacea* and *S. reticulata*, ca. 2500 m, 6 Sep 2001, *C. Ferrari & P. G. Jamoni EF40/01* (holotype: herbarium of E. Ferrari Verbaniae Sunae, Italy [n.v]; isotype: Gruppo Mic. Fara Nov. 3142 [n.v.]).

Pileus 20–30 mm wide, obtusely conical, conical to campanulate, expanding with age, at times with a low broad umbo, margin decurved; surface tacky viscid when moist and at times with adhering debris, smooth to finely fibrillose, on occasion excoriate-scaly around the center; disc whitish, pallid, or very pale brown due to the conspicuous velipellis there, brown or brown with a vinaceous tone (Wood Brown to Avellaneous) to yellowish brown (5YR 5/3–5/4 to 10YR 5/4) towards the margin, edge sometimes whitish when young; flesh thin, pallid, unchanging where bruised, odor spermatic when first cut, later somewhat unpleasant, or not remarkable. Lamellae adnexed, moderately close with several tiers of lamellulae, medium; grayish to pale brown in youth, becoming yellowish brown; edges pallid-fimbriate. Stipe 30–65 × 3–6 mm, terete, with a slight marginate or more rounded bulb, this up to 11 mm wide; surface dry, cortina absent, pruinose the entire length with a satiny streaked appearance; upper part salmon to ochraceous (or Light Vinaceous-Buff), whitish below, becoming light yellowish brown throughout with age, bulb white; solid, flesh colored like the surface, white in the bulb.

Basidiospores 7–*8*–9(9.5) × (4.5)5–*5.5*–6(7) µm, Q=(1.05)1.18–*1.47*–1.80(1.94) (n=69/7), angular, pentagonal to rectangular, mostly with 6–9 small or moderate-sized nodules, pale yellowish brown, apiculus small but distinct. Basidia 25–36 × 7–9 µm, 4-sterigmate, clavate, hyaline. Pleurocystidia 48–72 × (11)13–20 µm, fusiform, (sub)utriform, to subcylindric, lacking any conspicuous necks; thick-walled, walls 2–5 µm thick, pale yellowish; apices obtuse, crystalliferous. Cheilocystidia similar to pleurocystidia, walls more often thickened in the neck and tapering abruptly toward the apex and base, mixed with paracystidia. Caulocystidia similar to hymenial cystidia, mixed with cauloparacystidia and descending entire length of stipe. Pileipellis a cutis of repent, narrow, cylindric hyphae, these mostly smooth, at times with faint incrustations, hyaline or very pale to pale brownish overall in mass, most hyphae 5–10 µm wide. Clamp connections present.

Distribution and habitat.—Scattered singly on acid soil under conifers (*Picea*, *Abies*) and birch (*Betula*) in eastern North America, also with *Pinus* and dwarf *Salix* in Europe.

Phenology.—August to September.

Etymology.—The name *grammata* refers to the streaked-pruinose appearance of the stipe.

Additional specimens examined.—**NORWAY**. **Oppland**: Lunner, S. Oppdalen, on soil under *Picea abies* in eutrophic spruce forest, middle boreal zone, 400 m elev., 19 Aug 2002, *P. B. Matheny PBM2387* (WTU).

UNITED STATES. **New Hampshire**: Coos Co., Dixville Notch State Wayside Baby Flume Picnic Area, solitary on acid soil in disturbed woods under *Picea*, *Tsuga*, *Betula*, 7 Aug 2004, *P. B. Matheny PBM2558* (TENN-F-062401, muscarine bioassy). **New York**: Essex Co., Lake Placid, in lawn on acid soil under *Abies*, *Betula*, 518 m, 10 Aug 2020, *R. A. Swenie PBM4623* (TENN-F-075793). **North Carolina**: Yancey Co., Mount Mitchell State Park, Balsam Nature Trail, on acid soil under *Abies fraseri*, 1950 m, 28 Sep 2018, *R. A. Swenie PBM4210* (TENN-F-074617); Mount Mitchell State Park, ranger station area, in grass on acid soil under young *A. fraseri*, 1900 m, 12 Jul 2019, *P. B. Matheny & M. Hopping PBM4272* (TENN-F-074834); ibid., 21 Aug 2020, *M. Hopping PBM4447* (TENN-F-075319); ibid., 19 Sep 2020, *M. Hopping PBM4503* (TENN-F-075375). **Tennessee**: Sevier Co., Great Smoky Mountains National Park, Newfound Gap, solitary on acid soil under *Betula*, *Picea*, ca. 1500 m, 7 Sep 2004, *P. B. Matheny PBM2602* (TENN-F-062440).

Notes.—*Inocybe grammata* is a widespread species occurring in Europe and eastern North America. We studied fresh material from New York in Essex County near the type locality (North Elba) that conforms with *I. albodisca* and confirms the synonymy between *I. grammata* (which has priority) and *I. albodisca* (junior synonym) first suggested by Kühner (1933) and later reinforced by Vauras (1997). Other workers had maintained their separation (Stuntz, 1947; Moënne-Loccoz et al., 1990; Bon, 1998), but this is no longer justified (see also Crous et al., 2019 under discussion of *I. grammatoides*). ITS sequencing of the Lake Placid, New York material confirms a phylogenetic match with several samples of *I. grammata* from France, Italy, Spain, and Sweden (Fig. 1). *Inocybe acriolens* also occurs in the general area, but plant host association may best serve to distinguish it from *I. grammata*, as we are primarily aware of *I. acriolens* occurring under *Tsuga* and *Pinus*. Because Peck (1898) specifically cited the type of *I. albodisca* as having been found under spruce and balsam fir, and our sequenced material from New York, New Hampshire, and North Carolina occurred under *Abies* and/or *Betula*, we accept that these materials conform to *I. albodisca*. In addition, our observations of key microscopic features agree in all particulars with unpublished notes of the holotype collection of *I. albodisca* made by L. R. Hesler at the University of Tennessee and notes by Vauras (1997).

We also confirm that a portion of the isotype of *Inocybe permucida* Grund & Stuntz, described from Nova Scotia in mixed woods (Grund & Stuntz, 1983), is identical with *I. grammata*. In North America *I. grammata* is not uncommon, and we have confirmed its occurrence in southeast Canada, the northeast U.S., and in the southern Appalachians at high elevations.

Grund and Stuntz (1975) ascribed an equal stipe and penetrating odor to *Inocybe acriolens*, features deviating from *I. grammata*, but we have not found these traits to be consistent from collection to collection for *I. acriolens*. Rather, we expect *I. acriolens* can be distinguished from *I. grammata* based on habitat (*I. acriolens* occurs under hemlock and pine or in mixed deciduous forests) and perhaps by the pileus margin that, when fresh, appears decidedly covered with abundant superficial fibrils. Phylogenetically, the two species form separate species-level clades (Figs. 1, 2, 3). *Inocybe albodiscoides* differs from *I. grammata* by the larger and more robust basidiomes and decidedly smaller spores (mostly 5–6.5 × 4.5–5.5 μm), however, the pileus of *I. grammata* in the boreal zone of Europe may reach up to 60 mm wide (Jacobsson & Larsson, 2012).

The isotype of *Inocybe permucida* was found to be mixed confirming one element as *I. grammata* and a second element as *Pseudosperma aurora* (Grund & D.E.Stuntz) Matheny & Esteve-Rav. The protologue features illustrations of the *I. grammata* element, but the gross morphological description includes some elements (e.g., odor) of the *Pseudosperma* element and is thus chimeric.

The photo of *Inocybe albodisca* SAT-04-274-06 from Washington state is actually of a member of the *Inosperma maculatum* group (Trudell & Ammirati, 2009). Phillips (2005) depicted two different collections made in North America as *I. albodisca*, but habitat and geographic data were not provided; one could represent *I. velicopia*.

Field guides such as Baroni (2017) indicate that *Inocybe grammata* (as *I. albodisca*) is "considered poisonous" presumably due to the presence of the toxin muscarine. However, Kosentka et al. (2013) showed that one sample of *I. grammata* from New Hampshire (PBM2558) lacked muscarine.

Three European varieties of *Inocybe grammata* have been described: *I. grammata* var. *rubescens* R.Heim, *I. grammata* var. *chamaesalicis* Bon & Ferrari, and *I. grammata* var. *campanellispora* E.Ludw. A paratype of *I. grammata* var. *chamaesalicis* was sequenced (ITS region) in Crous et al. (2019) and shown to cluster with other ITS sequences of *I. grammata*, hence its consideration as a synonym of *I. grammata* here. DNA data were not available for the two other varieties.

Inocybe grammatoides Esteve-Rav., Pancorbo & E.Rubio, Persoonia 42: 419 (2019).—Type: Spain, Asturias, Ribadedeva, Pimiango, 39 m, in humus of very humid *Quercus ilex* subsp. *ilex* forest, with *Crataegus monogyna* shrub in calcareous soil, 26 Nov 2016, *P. Zapico s.n.* (holotype: AH 46618 [n.v.]; isotype: ERD-6897 [n.v.]. GenBank ITS = MK480531. (Fig. 7.)

References.—For a Description and Illustration of North American Material, See Also Grund and Stuntz (1980) as *Inocybe* "*albodisca*"

Distribution and habitat.—On soil under *Populus tremuloides* in southeast Canada and northern regions of the U.S., possibly also with *Quercus* and/or *Pinus strobus*; also central Europe (Germany, Spain). Under *Quercus* and other hardwoods in Europe and east Asia (Korea), also under *Pinus* in China.

Phenology.—July to August.

Etymology.—Named *grammatoides* due to similarity with *Inocybe grammata*.

Additional specimens examined.—**CANADA. Nova Scotia**: Kings Co. Lloyds, on bare soil in mixed *Betula*, *Fagus*, *Acer*, *P. tremuloides*, 30 Aug 1976, *K. A. Harrison s.n.* (ACAD-11762F).

UNITED STATES. Maine: York Co., Kennebunk, private residence, on soil in lawn bordered by mixed *Quercus*, *P. strobus*, *Ulmus* woods, 26 Jul 2021, *L. V. Kudzma LVK21232* (pers. herb.). **New York**: Essex Co., Lake Placid, 4589 Cascade Road, on acid soil in lawn near mixture of *Abies*, *Picea*, *Populus*, *Betula*, 14 Aug 2021, *L. V. Kudzma LVK21312* (pers. herb.). **Pennsylvania**: Carbon Co., Hickory Run State Park, on lawn with *Picea* present near a wood border of mixed woods, 15 Aug 2021, *D. Wasilewski LVK21459* (Mushroom Observer #466065) (pers. herb.).

Notes.—*Inocybe grammatoides* has not been previously reported from North America, however, phylogenetic analysis of the specimen ACAD11762, ascribed originally to *I. albodisca* in Grund and Stuntz (1980), revealed it within a cluster of samples, some identified as *I. grammatoides* and others as unidentified environmental samples, from Europe and North America (Fig. 1). All of the North American samples were derived from either ectomycorrhizal root tips of *Populus*, including *P. tremuloides*, or from the rhizosphere of *Populus* with exception of one sample, which may have been associated with *Quercus* and/or *P. strobus*. ACAD-11762F was collected under a mixture of hardwoods including *P. tremuloides*. In Europe *I. grammatoides* is regarded as an associate of hardwoods, namely *Quercus* (Crous et al., 2019), although our phylogenetic analysis also included samples associated with *Pinus* in this species-level clade (Fig. 1).

North American *Inocybe grammatoides* is illustrated in Grund and Stuntz (1980) based on observations from ACAD-11762F and shown here based on material collected in Maine (Fig. 7). The species is very similar in outward appearance to *I. acriolens*

Fig. 7. *Inocybe grammatoides*. Basidiomes of *LVK21232* from Maine (photo by L.V. Kudzma).

and *I. grammata* and features at times a pale margin because of the presence of a persistent white superficial layer, as in these two species. The spores are mostly 6.5–8 × 4.5–6 μm with 7–9 small nodules about an angular outline. The association with *Populus* in North America, and the clustering of our sequence with several environmental ITS sequences produced from *Populus* ectomycorrhizas and rhizosphere, seems to be unique. In Europe *I. grammatoides* is distinguished from *I. grammata* by the absence of a marginate base (however, a marginate base was present in ACAD-11762F) and more slender cystidia with a less thick wall (Crous et al., 2019). Admittedly, the microscopic features overlap with *I. grammata* a great deal; habitat, plant association, and the unique phylogenetic placement appear best to distinguish *I. grammatoides* from *I. grammata* and *I. acriolens*. Phylogenetic analyses of three different gene regions (ITS+28S, *rpb2*, *rpb1*) all show robust support for a sister group relationship between *I. grammatoides* and *I. acriolens* (Figs. 1, 2, 3).

Inocybe grammatoides was recently reported from Korea in deciduous woods by Cho et al. (2021).

Inocybe panamica Matheny & Corrales, **sp. nov.**—Type: Panama, Chiriqui: Fortuna Forest Reserve, Zarciadero, singly or scattered on soil in *Quercus* and *Oreomunnea mexicana* forest, 20 Mar 2012, *A. Corrales AC59* (holotype: UCH [!]). GenBank ITS = ON116987. MycoBank MB843512. (Figs. 8, 10I–J.)

Diagnosis.—Similar to other species in *Inocybe* sect. *Albodiscae* but occurring with *Quercus* and/or *Oreomunnea* in Central America. Most similar to *I. velicopia* but differs from it mainly by unique phylogenetic placement and molecular barcode (ITS) divergence (93% similarity).

Pileus 16–50 mm wide, convex to plano-convex, expanding with age with uplifted margins, at times with a low broad umbo, margin decurved to nearly straight; surface dry, smooth, at times somewhat excoriate-scaly or squamulose around

Fig. 8. *Inocybe panamica*. **A.** Basidiomes of *AC59* from Panama (holotype UCH). **B.** Basidiomes of *REH7181* from Costa Rica (NY). Scale bars = 1 cm.

the disc, weakly sulcate towards the margin (halfway to disc); disc pallid or cream-colored to pale yellow due to the distinct velipellis, margin brownish cream, yellowish cream to grayish cream or dark tan (6D5); flesh 2–4 mm thick under the center, white, unchanging where cut or bruised, odor mild. Lamellae sinuate, adnexed to barely so, or uncinate, moderately close with several tiers of lamellulae; dark cream or brownish white when young, becoming cinnamon to brown or dark tan (6D5) with age, ventricose, becoming broad and 2–7 mm deep, edges indistinctly pallid-fimbriate. Stipe 34–70(100) × 3–8 mm, terete, almost equal or with a weak marginate basal bulb; surface dry, densely pruinose with a fine satiny appearance the entire length; white to cream or becoming buff to light brown, or at times with a pinkish cinnamon cast, base with white mycelium; solid to hollow, flesh whitish or concolorous with the surface, white in the bulb.

Basidiospores (6)6.5–*7.4*–8.5(9.5) × (4)5–*5.6*–6(7.5) µm, Q (1.08)1.16–*1.34*–1.66(1.90) (n=61/4), angular-nodulose with mostly 5–9 moderate-size obtusely conic nodules, yellowish brown, with slightly thickened walls. Basidia 23–30 × 7–9 µm, 4-sterigmate, clavate, hyaline. Pleurocystidia 50–65(75) × 13–17 µm, fusiform to fusiform-ventricose; thick-walled, walls up 3.5 µm thick, light yellow; apices crystalliferous. Cheilocystidia similar to pleurocystidia, at times shorter. Caulocystidia 55–80(88) × 13–21 µm, similar to hymenial cystidia, in clusters and mixed with cauloparacystidia that feature slightly thickened walls (up to 1 µm thick) and a bulbous appearance (27–47 × 11–19 µm), descending entire length of stipe. Pileipellis a cutis of repent, narrow, cylindric hyphae, these mostly smooth, occasionally some hyphae with faint incrustations, hyaline or very pale to pale brownish overall in mass, most hyphae 2–10 µm wide. Clamp connections present.

Distribution and habitat.—Solitary or scattered singly on acid soil in *Quercus*-*Oreomunnea* forests at moderate to high elevations, Panama (type) and Costa Rica.

Phenology.— March to July, also November.

Etymology.—Named *panamica* (L.) in reference to the country name (Panama) of the type locality.

Additional specimens examined.—**COSTA RICA. Puntarenas**: Monteverde Cloud Forest Reserve, near the continental divide on Sendero Rio, under *Quercus*, 1590 m elev., 20 Nov 1993, *R. E. Halling REH7181* (NY01034372). **San José**: Dota Jardín, 3.5 km west of El Empalme, gregarious on soil under *Quercus seemannii*, *Quercus copeyensis*, 2200 m elev., *R. E. Halling & L. L. Norvell REH7995* (NY01034394).

PANAMA. Chiriqui: Fortuna Forest Reserve, 19 Apr 2012, *A. Corrales AC98* (ARIZ); ibid., 7 Jul 2012, *A. Corrales AC265* (ARIZ).

Notes.—Multiple samples of *Inocybe panamica* from Panama and Costa Rica form a strongly supported clade distinct from all other species in *I.* sect. *Albodiscae* (Figs. 1, 2), where the species is phylogenetically isolated from other Fagales-associated species. The Costa Rican collection REH7995 clusters with *I. panamica* with weak bootstrap support in the ITS+28S gene tree (Fig. 1) but with strong support in the *rpb2* gene tree (Fig. 2). Unfortunately, *rpb1* sequences from *I. panamica* were not generated. The ITS sequence from REH7995 differs from *I. panamica* at 16 positions (96% similarity). *Inocybe velicopia* (below) is very similar to *I. panamica* and may also feature an (acutely) umbonate pileus, but *I. velicopia* has not yet been confirmed from Panama and extends north into the U.S. (Indiana, New York, Tennessee, Wisconsin) where it has been recorded in association with *Quercus* and on root tips of *Castanea*. In Tennessee *I. velicopia* occurs on karst topography (limestone). In Panama, where basidiomes of *I. panamica* were collected, the soils there have been documented as acidic with a low pH (4.2) (Dalling & Turner, 2021). No obvious microscopic differences were noted between the two species, which are sympatric in Central America.

Inocybe velicopia Matheny & Kudzma, **sp. nov.**—Type: USA, Tennessee, Knox Co., West Knoxville, private residence at 7717 Twining Drive, scattered singly to gregarious on karst topography in lawn under mature *Quercus phellos* trees, 16 Oct 2009, *P. B. Matheny PBM3336* (holotype: TENN-F-063927 [!]). MycoBank MB843513. GenBank ITS = ON117000. (Figs. 9, 10K–L.)

Diagnosis.—Similar to other species in *Inocybe* sect. *Albodiscae* but occurring with *Quercus* and/or *Castanea* in eastern North America and Central America. Most similar to *I. panamica* but differs from it most readily by phylogenetic placement and molecular barcode (ITS) divergence (93% similarity).

Pileus 25–50 mm wide, conical to obtusely so, becoming plane with uplifted margins in age, at times umbonate with the umbo low and

Fig. 9. *Inocybe velicopia*. **A.** Basidiomes of *PBM3336* from Tennessee (holotype TENN-F-063927). **B.** Basidiomes of *LVK18101* from New York (Kudzma, pers. herb.). Scale bars = 1 cm.

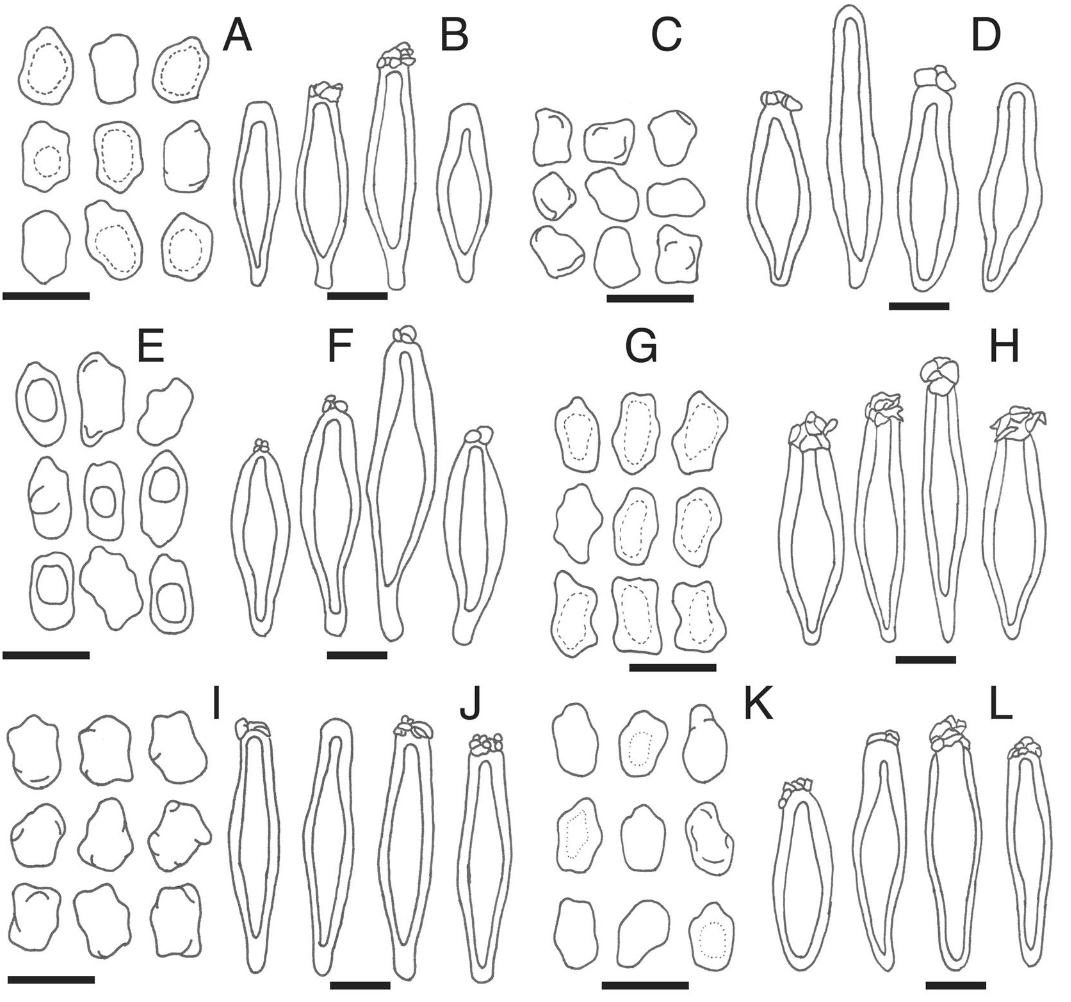

FIG. 10. Microscopic features of species of *Inocybe* sect. *Albodiscae*. **A.** Basidiospores of *I. acriolens* (*AWW270*). **B.** Pleurocystidia of *I. acriolens* (*AWW270*). **C.** Basidiospores of *I. albodiscoides* (*PBM554*). **D.** Pleurocystidia of *I. albodiscoides* (*PBM554*). **E.** Basidiospores of *I. floridana* (*PBM4529*). **F.** Pleurocystidia of *I. floridana* (*PBM4529*). **G.** Basidiospores of *I. grammata* (*PBM4272*). **H.** Pleurocystidia of *I. grammata* (*PBM4272*). **I.** Basidiospores of *I. panamica* (holotype). **J.** Pleurocystidia of *I. panamica* (holotype). **K.** Basidiospores of *I. velicopia* (holotype). **L.** Pleurocystidia of *I. velicopia* (holotype). Scale bars = 10 μm for spores, 20 μm for pleurocystidia.

obtuse, margin often decurved; disc smooth and greasy when moist, unbroken in youth, at times cracked with age; margin greasy, smooth to finely fibrillose, with small diffracted scales or lacerate-scaly with age, edge torn at times but not really rimose; disc whitish to cream (Ivory Yellow to Cartridge Buff), bicolorous, margin varying from light brown to umbrinous (Wood Brown to Tawny-Olive) or at times with a dull olivaceous tone; flesh pallid to light brownish gray, not changing color where bruised, 2–3 mm thick under the disc, thin elsewhere, odor spermatic. Lamellae adnexed to sinuate, close with several tiers of lamellulae; light gray when young to pale grayish brown, becoming pale brown to brown; edges pallid but indistinctly fimbriate. Stipe 40–65 × 5–8 mm at the apex, 9–13 mm across the distinctly marginately bulbous base; surface dry, pruinose the entire length, with a satiny-streaked appearance; most often with a pinkish cast, not white but Pale Ochraceous-Buff, Warm Buff, or Light Ochraceous-Buff, pallid or white just above the base; flesh colored like the surface, white in the bulb and just above.

Basidiospores (6)6.5–*7.3*–8.5 × 4.5–*5.2*–6(6.5) µm, Q 1.23–*1.41*–1.75 (n=40/2), angular-nodulose with mostly 7–9 small to moderate-sized nodules, yellowish brown, apiculus small but distinct. Basidia 26–33 × 7–9 µm, 4-sterigmate, clavate, hyaline. Pleurocystidia 55–60 × 17–20 µm, fusiform to fusiform-ventricose, generally with short necks, tapered below; thick-walled, walls up to 4.0 µm thick apically, walls pale yellow. Caulocystidia similar to cheilocystidia, abundant and descending the entire stipe length. Pileipellis a cutis of repent, narrow, cylindric hyphae, these mostly smooth, occasionally some hyphae with faint incrustations, hyaline or pale overall when viewed in mass, most hyphae 5–10 µm wide. Clamp connections present.

Distribution and habitat.—On karst topography under *Quercus* in lawns, mixed forests, and hardwood forests under *Quercus*, *Fagus*, and *Carya*, also recorded on root tips of *Castanea*. Widely distributed between Arkansas, Indiana, New York, Tennessee, and Wisconsin and southwards into lowland and high elevation oak forests in Costa Rica.

Phenology.—July to October.

Etymology.—Named *velicopia* (L.) referring to the distinct whitish to cream velum over the center of the pileus.

Additional specimens examined.—**COSTA RICA**. **Guanacaste**: 7 km northwest of Bagaces, in litter in *Quercus* forest, 80 m elev., Oct 1982 (no day), *LDG18697* (F as "*Inocybe* aff. *angustifolia*"). **San Jose**: Dota, La Chonta, south of Interamerican Highway near km 54 towards Laguna/Cerro Chonta, gregarious on soil under *Quercus seemannii* and *Q. copeyensis*, 2200 m elev., 11 Jul 2000, *R. E. Halling REH8024* (NY).

UNITED STATES. **New Jersey**: Stanton Station section south branch reservation, Flemington, 11 Aug 2012, *L. V. Kudzma LVK12095* (pers. herb.); on soil in mixed woods, Echo Hill Park, Lebanon, 7 Oct 2018, *L. V. Kudzma LVK18412X* (pers. herb.). **New York**: Bedford, I-684 Rest Area, on soil under *Quercus*, 27 Aug 2013, *L. V. Kudzma LVK13259* (pers. herb.); ibid., 20 Jul 2014, *L. V. Kudzma LVK14164* (pers. herb.); ibid., 5 Aug 2018, *L. V. Kudzma LVK18101* (pers. herb.); ibid., 4 Oct 2018, *L. V. Kudzma LVK18392* (pers. herb.); Rhinebeck, on soil under *Quercus*, *Carya*, *Fagus*, 23 Sep 2006, *J. C. Slot PBM2826* (TENN-F-065364); ibid., *PBM2829* (TENN-F-062620). **Tennessee**: Anderson Co., Norris Dam State Park, on karst topography under *Quercus*, *Carya*, *Fagus*, 29 Sep 2012, *P. B. Matheny PBM3911*; Knox Co., west Knoxville, private residence at 7717 Twining Drive, scattered singly to gregarious on karst topography in lawn under mature *Q. phellos* trees, 16 Oct 2009, *P. B. Matheny PBM3337* (TENN-F-063893).

Notes.—*Inocybe velicopia* is a newly described species in *I.* sect. *Albodiscae* characterized by the bicolorous pileus with a light brown to umbrinous margin and association with *Quercus* and *Castanea* in the eastern U.S. and with *Quercus* in Costa Rican oak forests, including high elevation and lowland tropical areas. The plant association will distinguish it from most other species in *I.* sect. *Albodiscae* other than *I. panamica*. *Inocybe grammatoides* has been noted in association with *Quercus* in Europe but not yet in North America where it appears to associate principally with *P. tremuloides*. *Inocybe floridana* differs from *I. velicopia* microscopically by the considerably longer spores.

Gene phylogenies of ITS+28S and *rpb2* serve to distinguish *Inocybe velicopia* from *I. panamica*. The two species co-occur in Costa Rica. *Inocybe velicopia* forms a strongly supported monophyletic lineage based on rDNA and *rpb1* analyses (Figs. 1, 3), but the *rpb2* gene tree recovered *I. velicopia* as a weakly supported paraphyletic group (Fig. 2). It appears the *rpb2* locus evolves more slowly than the nuclear rDNA region in this group and is characterized by a high number of single nucleotide polymorphic sites and potentially large population size across a wide geographic distribution (Costa Rica to northern regions of the U.S.). Indeed, of the seven *rpb2* samples, polymorphic positions were observed at 20 sites consistent with an incomplete lineage sorting process among populations of *I. velicopia*. Despite these attributes of the *rpb2* gene and the lack of exclusive reciprocal monophyly (Knowles & Carstens, 2007) among all three unlinked loci studied, *I. velicopia* can be distinguished from other species in *I.* sect. *Albodiscae* by a combination of morphological, ecological, and genetic data.

Siegel and Schwarz (2016) include a photo of a species in the *Inocybe albodisca* group that resembles specimens of *I. velicopia* shown here in Fig. 9B. The California specimens were recorded under oak. The reported spore dimensions also overlap with those of *I. velicopia*, but the stipe is described as white to beige and developing orange stains with age. Without sequence data of the California material, it is not possible to ascertain its taxonomic status further.

KEY TO THE SPECIES OF *INOCYBE* SECT. *ALBODISCAE* IN NORTH AND CENTRAL AMERICA

1. Basidiomes large and robust (pileus 20–60 mm wide; stipe base 8–14 mm broad); spores mostly 5–6.5 × 4.5–5.5 µm; under Douglas fir and/or Western Hemlock in the Pacific Northwest................*I. albodiscoides.*
1. Basidiomes smaller than above and/or spores longer than above; occurring in eastern North America and/or Central America................2.
   2. Spores 8.5–11.5 × 5–6 µm with few nodules, on karst topography in mixed pine-oak forests in northern Florida................*I. floridana.*
   2. Spores shorter than above, occurring in different areas or habitats................3.
      3. Occurring in Panama and Costa Rica on acidic soil in oak and oak-*Oreomunnea* forests................*I. panamica.*
      3. More widespread than above or occurring in temperate regions with various plant associates on acidic or calcareous soils................4.
         4. Under aspen in southeast Canada and in the northern U.S................*I. grammatoides.*
         4. Under oak, birch, or conifers................5.
            5. Widespread under oak or chestnut throughout eastern North America (on karst topography) and Central America................*I. velicopia.*
            5. Association with conifers or birch on acidic soils................6.
               6. Under hemlock and pines in northeast U.S. states and southeast Canada, pileus margin often with persistent pallid superficial fibrils, stipe base tending to indistinctly bulbous or without a bulb................*I. acriolens.*
               6. Under spruce, fir, and birch, southeast Canada to high elevation fir forests in the Southern Appalachians, pileus margin with pallid superficial fibrils but not as persistent as above, stipe base tending to marginately bulbous................*I. grammata.*

Notes.—*Inocybe vestalis* is a European species that lacks the distinct pallid pileal disc, has relatively short spores, and association with *Picea*, *Abies*, and *Fagus* on calcareous soils (Bandini et al., 2020). Two additional European species, *I. pargasensis* (Vauras, 1997) and *I. entolomatospora* (Bidaud et al., 2012) may also belong to *I.* sect. *Albodiscae*, but molecular confirmation is lacking for both.

Discussion

The goals of this study have been to document the taxonomic diversity of North and Central American taxa within the *Inocybe grammata* group. Eight species are recognized here, three of which (*I. grammata*, *I. grammatoides*, *I. vestalis*) occur in Europe and seven of which, three described as new, occur in North and/or Central America. The latter include *I. acriolens*, *I. albodiscoides*, *I. floridana*, *I. grammata*, *I. grammatoides*, *I. panamica*, and *I. velicopia*. Additional novel taxa or geographic expansions are expected or have been found in Asia (e.g., *I. grammatoides*). Accordingly, with now eight species formally recognized in the group, a new section, *I.* sect. *Albodiscae*, is described to accommodate them, and future studies may add more taxa. Almost all are characterized by the presence of a distinct velipellis that imparts a whitish or conspicuously pale disc on the pileus, an entirely pruinose stipe typically with a bulbous or indistinct marginate base and often with a flush of pink, angular-nodulose basidiospores, thick-walled cystidia, and a variety of plant host associations with Fagales, Salicaceae, Betulaceae, and Pinaceae. Only *I. vestalis* deviates from the others by the absence of any notable white or pallid disc.

The phylogenetic placement of *Inocybe grammata* and allies with respect to other lineages of *Inocybe* has not been clear or thoroughly addressed. In a study by Ryberg et al. (2010), one sample of *I. grammata* is indicated in a three-gene phylogeny (ITS, 28S, mtSSU rDNA) but without a clade designation. There *I. grammata* is recovered as a lineage sister to rest of *Inocybe* (their *I.* subg. *Inocybe*). In a separate study by Kropp et al. (2010) one sample of *I. albodiscoides* (as *I.* "*albodisca*") clustered among a large number of otherwise smooth-spored species based on analysis of 28S, *rpb1*, and *rpb2* gene regions. However, this analysis was flawed in that it included, unknown at the time, an *rpb1* paralogue of *I. albodiscoides*. An inclusive and densely sampled study of *rpb2* gene sequences by Matheny and Kudzma (2019) revealed the poorly placed position of five samples of *I. acriolens*, *I. albodiscoides*, and *I. velicopia* as sister to a group of nodulose-spored species including *I. stellatospora* and *I. chelanensis* of what now can be recognized as the *I. soluta* group but with weak support. It is expected that multiple gene studies will prove necessary to resolve, if possible, the phylogenetic placement of *I.* sect. *Albodiscae* with respect to other lineages within *Inocybe*. This task is complicated, however, by *rpb1* gene sequences of *I. albodiscoides*, all of which are paralogues and include a confirmed pseudogene sequence. This revelation best explains the phylogenetic discrepancy between the position of the group in Kropp et al. (2010) compared to Ryberg et al. (2010). Nevertheless, the clade is coherent as a whole and separated from other notable nodulose-spored species characterized by a pruinose stipe with a usually distinct marginate bulb.

This study also reveals other instances of genealogical discordance. The paraphyly of *Inocybe velicopia* in the *rpb2* gene tree and the relatively large number of single nucleotide polymorphisms, combined with the widespread geographic distribution in North and Central America, suggests that this species has undergone incomplete lineage sorting, and the time necessary for coalescence of all alleles, combined with a large population size, has not yet been achieved at this locus. However, ITS, 28S, and *rpb1* analyses, given the available data, do support the monophyly of *I. velicopia*. In addition, strongly supported topological conflict was noted between the ITS+28S and *rpb1* gene trees. For this reason, and because *rpb1* orthologues of *I. albodiscoides* were not recovered, we chose not to concatenate the three unlinked gene regions we sequenced. Lastly, multiple unlinked gene data are lacking for *I. vestalis*, which will prove necessary to ensure its classification within *I.* sect. *Albodiscae.*

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Declarations

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary Information

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