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Gymnopilus dilepis and *G. lepidotus* (Agaricales, Basidiomycota): synonym or not?

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Abstract

Currently described as part of Hymenogastraceae, *Gymnopilus* comprises up to 200 species distributed around the world, and 23 of these are found in Brazil. In this study, we discovered interesting specimens of *G. dilepis* growing with *Zoysia japonica* (Poaceae) grass in an urban area in the State of Paraíba. Originally described from Sri Lanka, this report treats a new and interesting record of this entity from Brazil. We also discuss whether to consider *G. lepidotus* as a synonym of *G. dilepis* based on morphological and phylogenetic evidence. Thus, as conclusion we prefer to maintain them as distinct entities and our material as *G. dilepis* based on morphological and ecological aspects.

Introduction

Gymnopilus P. Karst (1879: XXI) is a genus comprising about 200 worldwide distributed species (He et al. 2019; Wijayawardene et al. 2020). For many times, it was treated in the family Cortinariaceae (e.g., Singer 1951, 1986, Pegler 1983), but alternative classification included it in Strophariaceae because of the presence of styrylpyrone, the yellow pigment also found in *Pholiota* (Fr.) P. Kumm. and *Hypholoma* (Fr.) P. Kumm., genera traditionally included in this last family (Kühner 1984, Singer 1986). Recent studies treated the genus as independent family, although not yet formally described (Kalichman et al. 2020: 431), or in the family Hymenogastraceae (He et al. 2019, Tian & Matheny 2021).

In Brazil at least 23 species are known in the states of Amazonas, Mato Grosso do Sul, Paraíba, Paraná, Pernambuco, Rio Grande do Sul, Santa Catarina, and São Paulo. In state of Paraíba three taxa are known: *G. purpureograminicola* Silva-Junior & Wartchow, *G. purpureosquamulosus* Høil., and *G. subtropicus* Hesler (Magnago et al. 2015, Silva-Junior & Wartchow 2015, Fabrini & Wartchow 2020, Valões-Araújo & Wartchow 2021).

Some tropical species are widely distributed, as for example *G. purpureosquamulosus* described from Africa (Høiland, 1998), and then also referred in Europe, Neotropics (Guzmán-Dávalos et al. 2008, Magnago et al. 2013), and more recently Asia (Acharya et al. 2017). Continuing the recent inventories of *Gymnopilus* in Brazil (Silva-Junior & Wartchow 2015, Fabrini & Wartchow 2020, 2023, Fabrini et al. 2022), interesting specimens were discovered in a public lawn in the municipality of João Pessoas-PB and identified as *G. dilepis*. They are fully described and discussed here. We also discuss about the possible synonymization of *G. lepidotus* with *G. dilepis* based on previous morphological studies by Guzmán-Dávalos (2003) and molecular data provided here.

Material and Methods

Site collection and morphological analysis

The species was found associated with grass in a public lawn in the Campus of the 'Universidade Federal da Paraíba', and the brief description of that area is summarized in Silva-Junior & Wartchow (2015). Colour codes follow Kramer – OAC (2004)'. The observations of microscopic structures were made from material mounted in 3% KOH, Melzer's reagent, and Congo red solutions, following Hesler (1969). Description of the basidiospores follows the methodology proposed by Tulloss et al. (1992), slightly modified here. Measurements and statistics are based on 25 basidiospores. Abbreviations include L(W) = average basidiospores length (width), Q = the length: width ratio range as determined from all measured basidiospores, and Qm = the Q value averaged from all basidiospores measured. The exsicatum is deposited at JPB (Thiers 2022).

Genetic analysis

To confirm our specimen's identification, the whole genomic DNA of the specimen was extracted using the DNeasy Plant Mini Kit (Qiagen, Germany). PCR amplifications were done for complete internal transcribed spacers 1 and 2 and the 5.8S rDNA, called from here as ITS bounded by primers ITS5 and ITS4 (White et al. 1990). PCR conditions followed Xu et al. (2020). PCR products were unidirectional sequenced in ABI 3130 Genetic Analyzer (Applied Biosystems).

We used Geneious v9.1.3 (Kearse et al. 2012) to check the sequence quality of the strands by comparison to their respective chromatograms and to assemble and edit if necessary. GenBank sequences were also incorporated following close related sequences (lepidopus-subearlei and aeruginosus-luteofolius groups) indicated by Guzmán-Dávalos et al. (2003). To identify our samples, we assigned it to a species through a nucleotide Blast approach conducted in GenBank (http://blast.ncbi.nlm.nih.gov) and through a phylogenetic method (Bayesian tree).

The obtained sequences were analyzed by Standard Nucleotide Blast to find the most closely related species (**Table 1**). In the phylogenetic analysis,

Table 1. List of sequences used in this study.

Taxon	ITS	Voucher	Country	References
Gymnopilus dilepis	OM996163	GP01	Brazil	This study
Gymnopilus dilepis	AY280980	R. Treu (IMI-370900)	Malaysia	Guzmán-Dávalos et al. 2003
Gymnopilus dilepis	AY386823	BA5	Australia	Rees et al. 2004
Gymnopilus dilepis	AY386824	Leech AR 406	United Kingdom	Rees et al. 2004
Gymnopilus dilepis	AY386825	UNSW 89/12	Australia	Rees et al. 2004
Gymnopilus dilepis	AY386826	UNSW 99/3	Australia	Rees et al. 2004
Gymnopilus dilepis	AY386827	UNSW 95/2	Australia	Rees et al. 2004
Gymnopilus dilepis	AY386828	CANB HL 70329	Australia	Rees et al. 2004
Gymnopilus dilepis	AY386829	BRI O'Leary 5	Australia	Rees et al. 2004
Gymnopilus dilepis	AY386830	UNSW 89/311a	Australia	Rees et al. 2004
Gymnopilus dilepis	FJ800363	LS1	China	Not published
Gymnopilus dilepis	KT368680	INM - 2 - 71867	Japan	Kasuya et al. 2016
Gymnopilus dilepis	KT368681	TNS - F - 61955	Japan	Kasuya et al. 2016
Gymnopilus dilepis	KT368682	TAKK 13.11.6.3.1 in SAPA	Japan	Kasuya et al. 2016
Gymnopilus dilepis	KT368683	TAKK 13.11.6.3.2 in SAPA	Japan	Kasuya et al. 2016
Gymnopilus dilepis	KU727215	TNS - F - 70390	Japan	Kasuya et al. 2016
Gymnopilus dilepis	KX639496	SDBR-CMU-NK0116	Thailand	Suwannarach et al. 2017
Gymnopilus dilepis	KX639497	SDBR-CMU-JK0142	Thailand	Suwannarach et al. 2017
Gymnopilus dilepis	MF195028	TW2AWP	Sri Lanka	Perera et al. 2021
Gymnopilus dilepis	MG937798	MushroomObserver. org/237083	USA	Not published
Gymnopilus dilepis	MH185801	Mushroom Observer # 314289	USA	Not published
Gymnopilus dilepis	MH211909	FLAS-F-61468	USA	Not published
Gymnopilus dilepis	MK214393	MHHNU 30975	China	Chen & Zhang 2019
Gymnopilus dilepis	MN622751	HFJAU-ND013	China	Not published
Gymnopilus dilepis	MN901949	PRM 946008	Malaysia	Not published
Gymnopilus dilepis	MT237518	TENN:056277	USA	Not published
Gymnopilus dilepis	MT945073	JZ72	undefined	Not published
Gymnopilus dilepis	MW619626	MC5	USA	Not published
Gymnopilus dilepis	OK446754	PC12	Philippines	Not published

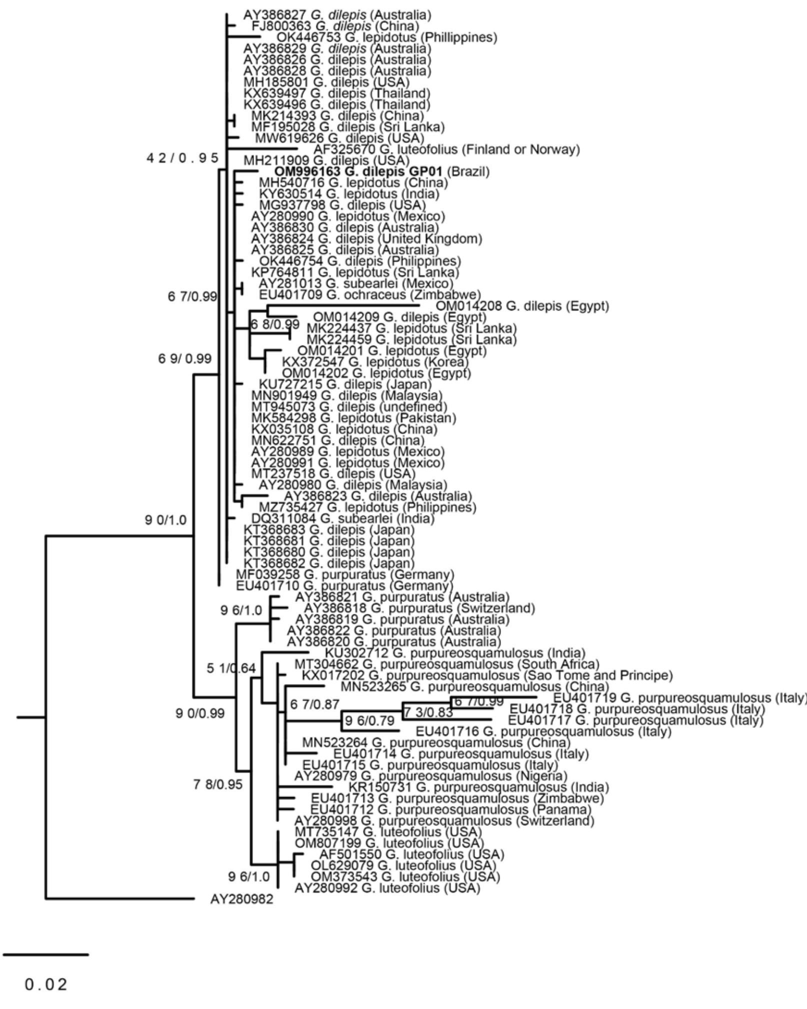
Taxon	ITS	Voucher	Country	References
Gymnopilus dilepis	OM014208	H210113-018_I20_S16-group8_FF-group8	Egypt	Not published
Gymnopilus dilepis	OM014209	H210113-018_K20_S16-group8_FR-group8	Egypt	Not published
Gymnopilus lepidotus	AY280989	G. Guzman 30374 (XAL)	Mexico	Guzmán-Dávalos et al. 2003
Gymnopilus lepidotus	AY280990	L. Guzman-Davalos 7868 (IBUG)	Mexico	Guzmán-Dávalos et al. 2003
Gymnopilus lepidotus	AY280991	G. Guzman 30602 (XAL)	Mexico	Guzmán-Dávalos et al. 2003
Gymnopilus lepidotus	KP764811	UOC-KAUNP-MK64	Sri Lanka	Not published
Gymnopilus lepidotus	KX035108	E140524	China	Not published
Gymnopilus lepidotus	KX372547	ASIS 27144	Korea	Seok et al 2016
Gymnopilus lepidotus	KY630514	KWGM 35	India	Not published
Gymnopilus lepidotus	MH540716	extr13	China	Not published
Gymnopilus lepidotus	MK224437	077_06_01	Sri Lanka	Not published
Gymnopilus lepidotus	MK224459	personal collection:Maduranga: AT_L12_E4ST1	Sri Lanka	Not published
Gymnopilus lepidotus	MK584298	B.B26	Pakistan	Bashir et al. 2018
Gymnopilus lepidotus	MZ735427	DQS57F	Philippines	Not published
Gymnopilus lepidotus	OK446753	PC10	Philippines	Not published
Gymnopilus lepidotus	OM014201	H210113-018_E20_P13-group8_FF-group8	Egypt	Not published
Gymnopilus lepidotus	OM014202	H210113-018_G20_P13-group8_FR-group8	Egypt	Not published
Gymnopilus luteofolius	AF325670	Ten21810	Finland or Norway	Moser et al. 2001
Gymnopilus luteofolius	AF501550	JFA 12367	USA	Rees et al. 2002
Gymnopilus luteofolius	AY280992	L. R. Hesler & H. Ford (DAOM-80626)	USA	Guzmán-Dávalos et al. 2003
Gymnopilus luteofolius	MT735147	Mushroom Observer 377656	USA	Not published
Gymnopilus luteofolius	OL629079	MushroomObserver.org/460047	USA	Not published
Gymnopilus luteofolius	OM373543	inaturalist.org/observations/102735959	USA	Not published
Gymnopilus luteofolius	OM807199	MushroomObserver.org/480086	USA	Not published
Gymnopilus ochraceus	EU401709	L. Ryvarden & K. Htiland G23 (O-72838, type)	Zimbabwe	Guzmán-Dávalos et al. 2008
Gymnopilus purpuratus	AY386818	ZT 02/01	Switzerland	Rees et al. 2004
Gymnopilus purpuratus	AY386819	UNSW 99/40	Australia	Rees et al. 2004

Taxon	ITS	Voucher	Country	References
Gymnopilus purpuratus	AY386820	BRSA 02/01	Australia	Rees et al. 2004
Gymnopilus purpuratus	AY386821	BRSA 02/11	Australia	Rees et al. 2004
Gymnopilus purpuratus	AY386822	UNSW 02/02	Australia	Rees et al. 2004
Gymnopilus purpuratus	EU401710	H. Reis s.n. (L-0109669)	Germany	Guzmán-Dávalos et al. 2008
Gymnopilus purpuratus	MF039258	SMNS:SMNS-STU-F-0900405	Germany	Eberhardt et al. 2018
Gymnopilus purpureosquamulosus	AY280979	Zoberi 342 M. H. Zoberi 342 [K(M) 75214]	Nigeria	Guzmán-Dávalos et al. 2003
Gymnopilus purpureosquamulosus	AY280998	O. Rollin 89-16 (IBUG)	Switzerland	Guzmán-Dávalos et al. 2003
Gymnopilus purpureosquamulosus	EU401712	C.L. Ovrebo 3594 (IBUG)	Panama	Guzmán-Dávalos et al. 2008
Gymnopilus purpureosquamulosus	EU401713	L. Ryvarden & K. Htiland G24 (O-72839, type)	Zimbabwe	Guzmán-Dávalos et al. 2008
Gymnopilus purpureosquamulosus	EU401714	A. Vizzini AV G-1 (IBUG)	Italy	Guzmán-Dávalos et al. 2008
Gymnopilus purpureosquamulosus	EU401715	M. Contu s.n (IBUG, type)	Italy	Guzmán-Dávalos et al. 2008
Gymnopilus purpureosquamulosus	EU401716	M. Contu s.n (IBUG)	Italy	Guzmán-Dávalos et al. 2008
Gymnopilus purpureosquamulosus	EU401717	M. Contu s.n (IBUG)	Italy	Guzmán-Dávalos et al. 2008
Gymnopilus purpureosquamulosus	EU401718	M. Contu s.n (IBUG)	Italy	Guzmán-Dávalos et al. 2008
Gymnopilus purpureosquamulosus	EU401719	M. Contu s.n (IBUG)	Italy	Guzmán-Dávalos et al. 2008
Gymnopilus purpureosquamulosus	KR150731	Ignatius 1	India	Not published
Gymnopilus purpureosquamulosus	KU302712	CUH:AM252	India	Acharya et al 2017
Gymnopilus purpureosquamulosus	KX017202	DED 8302 (SFSU)	São Tomé and Príncipe	Desjardin & Perry 2016
Gymnopilus purpureosquamulosus	MN523264	ZD16071203	China	Not published
Gymnopilus purpureosquamulosus	MN523265	ZD16061302	China	Not published
Gymnopilus purpureosquamulosus	MT304662	personal collection:M. van der Walt:VDW1598	South Africa	van der Walt et al. 2020
Gymnopilus subearlei	AY281013	G. Guzman 11648-A (ENCB, TYPE)	Mexico	Guzmán-Dávalos et al. 2003
Gymnopilus subearlei	DQ311084	RA-2M	India	Singh et al. 2006
Gymnopilus fulvosquamulosus	AY280982	D. Guravich 220 (MICH-42155)	USA	Guzmán-Dávalos et al. 2003

first, we aligned sequences using Muscle v3.8.425 (Edgar 2004), a module implemented in Geneious v9.1.3 with default settings. In our analysis, we included ITS sequences with more than 400 bp.

A Bayesian tree was calculated using the uncorrelated lognormal relaxed clock model implemented in BEAST 1.8.4 with an input file generated in BEAUti 1.8.4 (Drummond et al. 2012). Each analysis ran for 100,000,000 generations with a sample frequency of 1,000 and Yule process of speciation was applied as a tree prior. The model of evolution and partitioning schemes selected by jModel Test 3.0.4 (Posada 2008) in the BIC method was GTR+G. Effective sample sizes (ESS) were well-above 200 for all parameters and the final trees were calculated after 10% of burn-in. The parameters to Tree Annotator (Drummond et al. 2012) were Maximum Clade Credibility Tree setting, and the Medium Node height Setting. Support for nodes was determined using posterior probabilities (PP). The sequence was deposited in GenBank (NCBI) under number accession OM996163.

Fig. 1. Phylogenetic relationships for *Gymnopilus* (lepidotus-subearlei and aeruginosus-luteofolius groups) and closely related species based on nuclear ITS rDNA fragments. The Maximum likelihood bootstrap values and the Bayesian posterior probability for each of the nodes are provided from the left to the right of the slash, respectively (values shown only above 40% and 0.5).



Results

Genetic analysis

Considering a Query cover of 100%, our nucleotide Blast analysis showed that the specimen is close to sequences identified as *Gymnopilus lepidotus* (Per. ident. 99.38%, E-value 0.00; AY280991) from Mexico. In our phylogenetic tree (**Fig. 1**), the specimen was also close to sequences of *G. dilepis* and *G. lepidotus*, as well as *G. ochraceus* and *G. subearlei* from different continents.

Taxonomic Treatment

Gymnopilus dilepis (Berk. & Broome) Singer, Lilloa 22: 560. 1951. MycoBank #445575

≡ *Agaricus dilepis* Berk. & Broome, Bot. J. Linn. Soc. 11: 542. 1871.

≡ *Flammula dilepis* (Berk. & Broome) Sacc., Syl. Fung. 5: 812. 1887.

≡ *Naucoriua dilepis* (Berk. & Broome) Cout., Anais Inst. Sup. Agron. Univer. Téc. Lisboa. 2: 21. 1925.

= **(?)** ***Gymnopilus lepidotus*** Hesler, Mycol. Mem. 3: 40. 1969. MycoBank #314787

Figs. 2–3.

MATERIAL EXAMINED: Brazil, Paraíba, João Pessoa, UFPB Campus I, 02.IV.2019, F. Fabrini GP01 (JPB 66864).

Basidiomata small, subgregarious (**Fig. 2**). Pileus 12–33 mm in diam., plane; surface centrally glabrous yellowish (OAC816), squamulose toward margin, squamules reddish brown (OAC698); margin entire, non-sulcate nor striate; context fleshy. Lamellae adnate, subdistant to subclose, ferrugineous (OAC754), 2–4 mm broad; edge even, concolorous to side; lamellulae common, with diverse lenghts. Stipe 34–50 × 4–6 mm, central, subequal to narrowly clavate and compressed, pale yellowish (OAC807) overall length, surface longitudinally fibrillose, context, hollow; annulus membranous to subfibrillose, single edged; whitish mycelial pad present at base. Odor and taste not seen.

Basidiospores (**Fig. 3F**) 7.1–8.6 × 5.1–6.1 μm (L = 7.7 μm; W = 5.3 μm; Q = (1.27–) 1.33–1.55 (–1.60); Qm = 1.45), ellipsoid, yellowish brown in KOH, wall verrucose, thin walled. Basidia (**Fig. 3E**) 15.3–23.9 × 6.1–8.16 μm, clavate, hyaline. Pleurocystidia as frequent pseudocystidia (**Fig. 3B**), 15.8–29.6 × 4.6–8.7 μm, with yellowish brown pigment, thin-walled. Cheilocystidia (**Figs. 3C, 3D**) 21.4–26.5 × 4.1–7.1 μm, lageniform with capitulate apex, hyaline, thin-walled. Lamellae trama regular, hyphae 5.1–8 μm wide, hyaline or yellowish. Pileus trama (Fig. 3A) with radial to subradial construction, with thin-walled hyaline to yellowish hyphae. Pileipellis a differentiated cutis, hyphae with yellowish to yellowish brown pigment, with terminal cells 5.1–9.2 μm wide, thin-walled. Stipitipellis with caulocystidia 31.1–52 × 6.1–16.3 μm, hyaline, thin-walled. Clamp connections frequent.

HABITAT: Subgregarious among grass (*Zoysia japonica*) in an urban environment.

DISTRIBUTION: Asia, North America, South America (Paraguay), and now from Brazil.

Discussion

Gymnopilus dilepis was originally described as *Agaricus dilepis* by Berkeley & Broome (1871) growing on dead wood from Sri Lanka, with minute brown to tawny squamules on the pileus surface. Only recently, Thomas et al. (2003) and Suwannarach et al. (2017) referred to violet squamules in Indian and Thai specimens. *Gymnopilus lepidotus* was described by Hesler (1969) based on basidiomes without any reddish, purple or brownish squamules on pileus, but antimon-yellow ones. More recently, Campi et al. (2015) reported chestnut scales in Paraguayan specimens identified under this name.

Actually, the most complete type study of *G. dilepis* and *G. lepidotus* was performed by Guzmán-Dávalos (2003), who suspected both as being synonym. The only difference was the shape of the cheilocystidia (widely rostrate in *G. dilepis* and narrowly lageniform to utriform with long or short neck and capitate in *G. lepidotus*), and the distribution (paleotropical in *G. dilepis* and neotropical in *G. lepidotus*). In subsequent studies by Suwannarach et al. (2017: 339–340) two different shaped cheilocystidia

Fig. 2. *Gymnopilus dilepis*. Basidiomes *in situ* (bar = 20 mm).

were referred in Thai specimens of *G. dilepis*: (1) 'utriform, ranging from clavate with a wide rostrum' to (2) 'lageniform with a short neck and a non-capitate or subcapitate apex'. We need highlight here that in our specimens, we also found both types of cheilocystidia, even in the same sectioned lamellae (**Fig. 3D**).

Phylogeny of the ITS region showed our specimen having high identity with sequences of *G. lepidotus* from many countries belonging to different continents. Although many sequences of *G. dilepis* and *G. lepidotus* are separated in different branches, the molecular similarity among them is high and they clearly represent to a single species based in ITS region. Thus, it would be plausible to consider both names as synonym under *G. dilepis*, since the epithet '*dilepis*' (Berkeley & Broome 1871, Singer 1951) has priority over '*lepidotus*' (Hesler 1969) according to Shenzen Code (Turland et al. 2018). On the other hand, as already mentioned by Guzmán-Dávalos et al. (2008) and Desjardin & Perry (2016), the high similarity of the ITS sequences is not an exact reflection of the conspecificity, since the morphology can be highly variable.

Thus, the epithet '*dilepis*' is more frequently used for the specimens in Africa (e.g., Coutinho 1925) and Australasia (Pegler 1986, Treu 1998, Watling 1998, Thomas et al. 2003, Rees et al. 2004, Kasuya et al. 2016, Suwannarach et al. 2017, Lee et al. 2020), while '*lepidotus*' for the Americas entities (Guzmán-Dávalos 1996, 2002, Niveiro & Albertó 2014, Grassi et al. 2016, De la Fuente et al. 2020, Batallas-Molina et al. 2021, Campi et al. 2021). The last epithet, however, was used in some few recent works for specimens collected in Sri Lanka (Fernando et al. 2015) and Indonesia (Talukder & Sun 2017).

In some taxa of *Gymnopilus*, the pleurocystidia are defined as pseudocystidia due their chemically heterogeneous content (Singer 1986, Guzmán-Dávalos 2003). Regarding to size, they are similar in the type species of *G. lepidotus* and *G. dilepis*

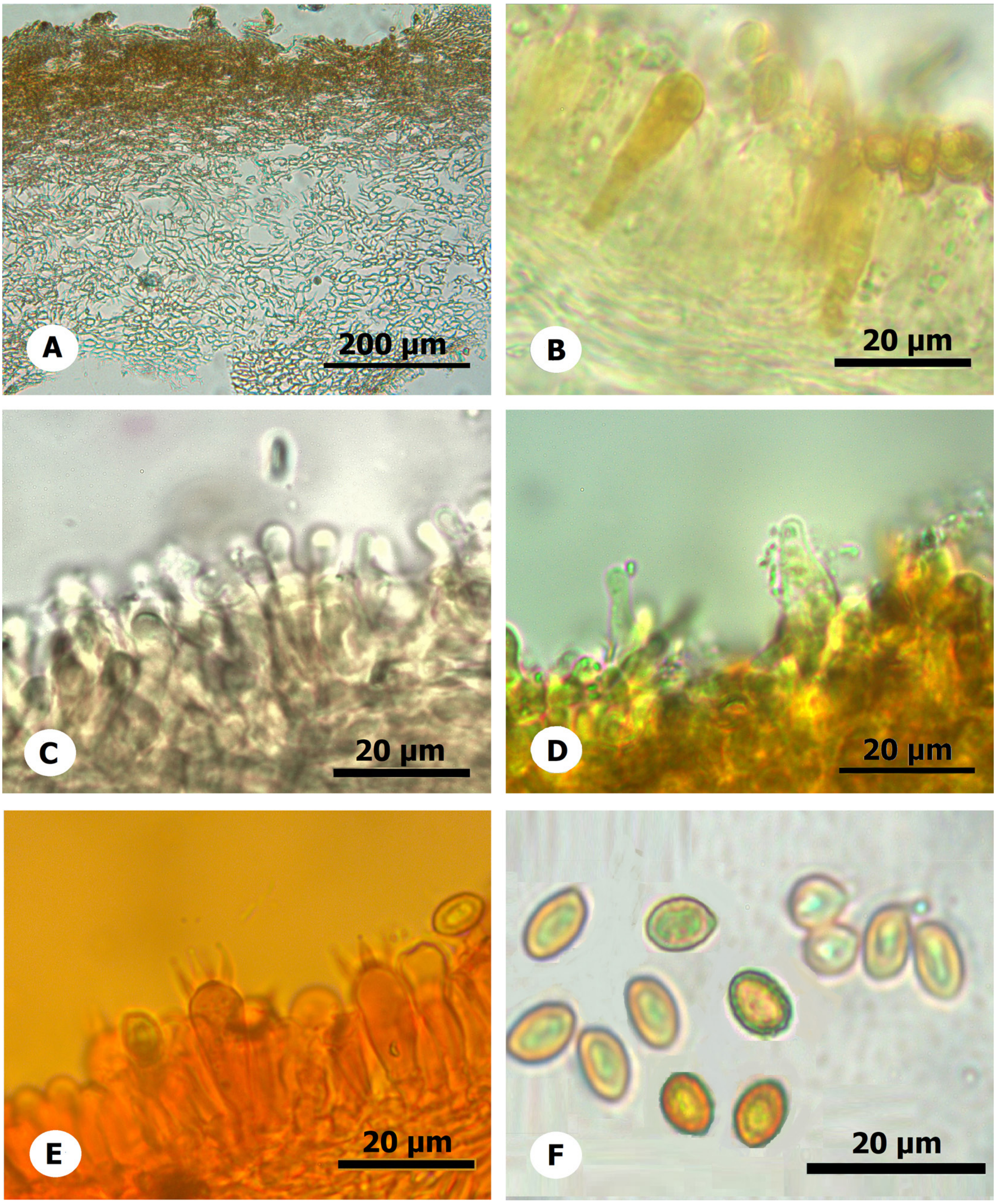


Fig. 3. *Gymnopilus dilepis*, all in in KOH 3% solution. **A.** Pileus trama showing the radial to subradial construction. **B.** Pseudocystidia. **C-D.** Cheilocystidia. **E.** Basidia and basidiospores in Congo Red solution. **F.** Basidiospores.

(Guzmán-Dávalos 2003). Hesler (1969), on the other hand, described *G. lepidotus* with obclavate to subventricose hyaline pleurocystidia measuring 28–40 × 5–6 µm, and referred flask-shaped and brown pigmented 'basidioles' measuring 24–28 × 5–6 µm. However, type studies by Guzmán-Dávalos (2003) referred these structures as 'pseudocystidia', who found 24–35.2 × 5.6–8 (–12.5) µm in *G. lepidotus*, and 20–27.2 × 7.2–8.8 µm in *G. dilepis*. Campi et al. (2021) referred the pseudocystidia 21.5–27.5 (–43.5) × 6–7.5 (–10) µm for *G. lepidotus* from Paraguay.

The recently described *G. purpureograminicola* from the same habitat might also be a synonym of *G. dilepis*, but in accordance to Hesler (1969), Silva-Junior & Wartchow (2015) also considered it as 'basidioles'. Unfortunately, the holotype of *G. purpureograminicola* was not able to be sequenced and this hypothesis is based only by morphology.

Regarding to substrate, our specimens of *G. dilepis* were found associated with a turfgrass named 'Emerald grass', an exotic ornamental plant known as *Zoysia japonica* Steud., originate from Japan (Steudel 1855) and used in residential or sports lawns in Brazil (Salvador & Minami 2002). The unpublished PhD thesis by Aguilar-Vildoso (2009) raised the question how the material molecularly identified by him as *G. dilepis* arrived in Brazil together with citrus seedling. We need take attention that previous few studies referred the Asian *G. dilepis* as frequently associated with coconut (Treu 1998, Watling 1998). Since the 'Emerald grass' is originally from Asia, it is quite probably that *G. dilepis* came attached to these seedlings, and it can clearly be considered as an exotic organism. Thus, basing in the morphological and ecological aspects, we consider our material as *G. dilepis*. From this work, it is evident that future multigene phylogenetic studies are needed for a better elucidation of the species concept among this genus.

Gymnopilus bryophilus Murrill and *G. subearlei* R. Valenz., Guzmán & J. Castillo also present pseudocystidia. However, they differ in the following features: the first species has distinctly smaller basidiospores 5.2–6.4 × (3.6–) 4–4.8 µm (Guzmán-Dávalos 2003) while *G. subearlei* differs at least in the narrow lageniform pseudocystidia and interwoven pileus trama (Valenzuela et al. 1981, Guzmán-Dávalos 2003).

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AUTHORS' CONTRIBUTIONS All authors contributed to the study conception and design. Samples, morpho-anatomical data, material preparation and analysis were performed by FF. The manuscript was written by FF, RK and FW, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Statements and Declarations

COMPETING INTERESTS. The authors declare that they have not incurred in conflicts of interest.

ETHICAL APPROVAL. The manuscript complies with the ethical rules applicable for this journal.

CONSENT FOR PUBLICATION. All the authors have given consent to the publication of this manuscript.

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