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Article

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Four new species of *Entoloma* (Entolomataceae, Agaricomycetes) subgenera *Cyanula* and *Claudopus* from Vietnam and their phylogenetic position

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Abstract

Three new species of *Entoloma* subgenus *Cyanula* (*Entoloma argus*, *E. arion*, and *E. icarus*) from Kon Chu Rang Nature Reserve and one species of subgenus *Claudopus* (*E. daphnis*) from Cat Tien National Park were discovered during an investigation of the diversity of the mycobiota of Central and South Vietnam and are described here. Illustrated descriptions of their macro- and microscopic features and discussion of similar taxa are given. Phylogenetic analysis was based on nrITS1-5.8S-ITS2 and nrLSU regions. The results confirm the polyphyletic origin of the pleurotoid basidiocarp form in the genus *Entoloma*.

Keywords: Agaricales, Basidiomycota, molecular phylogeny, pleurotoid basidiocarps, taxonomy

Introduction

The genus *Entoloma* (Fries 1838: 143) P. Kummer (1871: 23) *s.l.* is one of the largest agaricoid genera and contains ca. 1000 species described globally (Kirk *et al.* 2008). It is morphologically very diverse and comprises agaricoid, gasteroid, pleurotoid and cyphelloid forms (Co-David *et al.* 2009, Baroni & Matheny 2011).

The name *Cyanuli* was introduced by Romagnesi (1974) for the section within the genus *Rhodophyllus* Quélet (1886: 57) [= *Entoloma* (Fr.) P. Kumm.]. As we know, the taxonomy of the Entolomatoid fungi traditionally followed two directions. According to one, genus *Entoloma* is considered in the broad sense (*e.g.*, Romagnesi 1974, Noordeloos 1992, 2004) and consists of several subgenera, including subgenus *Leptonia* (Fries 1821: 10, 201) Noordeloos (1981: 146). The combination *Entoloma* section *Cyanula* (Romagn.) Noordeloos (1982: 452) was made in the framework of the subgenus *Leptonia*. The traditional morphology-based concept of *Entoloma* subgenus *Leptonia* (Noordeloos 1992, 2004) appeared to be polyphyletic (Co-David *et al.* 2009, Morozova *et al.* 2014), and accordingly section *Cyanula* was raised to the rank of *Entoloma* subgenus *Cyanula* (Noordeloos & Gates 2012). In concordance to the other opinion, *Leptonia* is considered as a separate genus (*e.g.*, Horak 1980, 2008, Largent 1977, 1994), and combinations *Leptonia* subgenus *Cyanula* (Romagn.) Largent (1994: 64) and *Leptonia* section *Cyanula* (Romagn.) Largent (1994: 65) have been made.

Entoloma subgenus *Cyanula* is characterized by the combination of a usually collybioid habit, more or less glabrous stipe and squamulose pileus, at least in the central part, heterodiametrical spores, absence of clamp connections and presence of brilliant granules in the trama.

A large-scale study devoted to this subgenus from the predominantly boreal-temperate zone of Eurasia, based on the concordance of molecular-genetic and morphological data, will be published in due course (Dima *et al.* 2022, in prep.). However, the diversity of this group in tropical Asia is also very large and underexplored. Many representatives of this group from Indomalaya are presented in the monograph of Horak (1980), and in a series of articles from Japan (Hongo 1989), India (Manimohan *et al.* 1995, 2002, 2006), and China (He *et al.* 2011, 2012, 2016, 2017). Furthermore,

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some *Cyanula* species from the Central Highlands of Vietnam have been described by Morozova *et al.* (2012) and in Crous *et al.* (2015, 2017).

Claudopus, considered a subgenus of *Entoloma* by some authors, *e.g*. Romagnesi (1974), and Noordeloos (1992, 2004), or a genus by others (*e.g*., Horak 1980, 2008, Largent 1994), was mainly used to accommodate species with pleurotoid basidiocarps with an eccentric, lateral or absent stipe, but occasionally also included species with omphaloid, and clitocyboid habits (Noordeloos 1992, 2004), and, according to the molecular data, even tricholomatoid basidiocarps (Co-David *et al.* 2009). Recent molecular studies have shown that like *Leptonia*, subgenus *Claudopus* in the former morphological sense is also polyphyletic (Vila *et al.* 2014, He *et al.* 2015, 2019). The current monophyletic concept of subgenus *Claudopus* is restricted to the species around *E. byssisedum* (Persoon 1800: 56) Donk (1949: 158), and *E. undatum* (Gillet 1876 [1878]: 407) M.M. Moser in Gams (1978: 211). The mainly omphalinoid species around *E. rusticoides* (Gillet 1876 [1878]: 425) Noordeloos (1981: 150) formerly in section *Undati* (Romagnesi 1974: 327) Noordeloos (1992: 613) (Noordeloos 1992, 2004) are rather distant and form a separate lineage (Vila *et al.* 2014).

The diversity of pleurotoid species of the subgenus *Claudopus* is higher than previously thought. Many new species are now being described from southeast Asia (Deng *et al.* 2015, He *et al.* 2015, 2019) and other regions of the world (Largent *et al.* 2011; Noordeloos & Gates 2012; Niveiro *et al.* 2021). The accumulation and analysis of more data will help resolve the phylogenetic relationships within this group more accurately.

Only a few species with a pleurotoid habit and blue basidiocarps are known from Asia, *viz*., *Entoloma cyaneomelaenum* (Boedijn 1929: 419) Manimohan, Leelavathy & Noordeloos (2002: 629) [as '*cyaneomelaenus*'], and *E. nubilum* Manimohan, Leelavathy & Noordeloos (2002: 626). The taxonomic position of these species was uncertain. Initially, the first species was placed in the genus *Claudopus* (Boedijn 1929; Horak 1980), however, Manimohan *et al*. (2002) pointed out that these species did not fit in the current concept of *Entoloma* subgenus *Claudopus* because of the blue plasmatic pigment and lack of encrusting pigments and suggested that they represent reduced forms of *Entoloma* section *Cyanula* species. They also suggested that a pleurotoid habit in *Entoloma* is polyphyletic and may have occurred several times during the evolution of the genus.

Three new species of *Entoloma* subgenus *Cyanula* (Romagnesi 1974: 328) Noordel., in Noordeloos & Gates (2012: 209) and one species of subgenus *Claudopus* (Gillet 1876 [1876]: 426) Noordeloos (1981: 147) were revealed during an investigation of the diversity of the mycobiota of Central and South Vietnam. Two of the newly described species have pleurotoid basidiocarps with eccentric and reduced stipe. The new species have been named after some butterfly species from the Lycaenidae (Cupidinidae) family, which in turn were named after the heroes of Greek mythology.

Material and methods

Collecting and site description

The material for this study was collected by authors during the expeditions of the Vietnam-Russian Tropical Research and Technological Centre (VRTC) to the Central Highlands of Vietnam and to the Cat Tien National Park in South Vietnam.

The Kon Chu Rang Nature Reserve is located on the Tay Nguyen Plateau in the northeastern part of Gia Lai Province of Vietnam, between 14.50°N–14.58°N and 108.5°E–108.65°E. The area of the reserve is 159 km^2, of which 156.1 km^2 (99 %) are primary and intact forests. The relief is hilly to mountainous in the northern part, with heights from 800 to 1452 m a. s. l. (Kon Chu Rang Mt). The average annual temperature is about 21 °C (from 28 °C in May to 12 °C in January). The average annual precipitation is about 1900–2000 mm with the peak in September (340 mm). The dry season is from January to April (New *et al.* 2002; Tordoff *et al.* 2004). Numerous rivers flowing through this territory belong to the basin of the Kon River (Sông Kôn) with a series of waterfalls, the most famous and tallest of which has a height of 50 m.

The main forest type in the reserve is middle-mountain evergreen broad-leaved and mixed forest dominated by Fagaceae (*Lithocarpus*, *Quercus*, *Castanopsis*), Lauraceae, Fabaceae, Clusiaceae, Myrtaceae, Ericaceae, Burseraceae, and Magnoliaceae, mixed with gymnosperms (*Dacrycarpus imbricatus*, *Dacrydium elatum*), distributed at elevations between 900 and 1500 m in the north-west of the nature reserve. Only 2 % of the nature reserve is covered by secondary vegetation, mainly scrub with scattered trees. The first data on the mycobiota of Kon Chu Rang Nature Reserve were published only recently, including those on *Entoloma* from other subgenera, and from the Boletaceae (Morozova *et al.* 2018; Crous *et al.* 2021a, b; Pham *et al.* 2021).

Cat Tien National Park is in the south of Vietnam, about 130 km north-east of Ho Chi Minh city in the administrative

areas of Dong Nai, Binh Phuoc and Lam Dong provinces. It is one of the largest national parks in Vietnam, with a total area of almost 720 km^2. In the east and southeast, the Dong Nai River forms the natural border of the park. The altitude of the park varies between 100 and 375 m above sea level. The soil mainly consists of deep fertile red basalt soils with numerous stony outcrops. The area is submitted to a typical tropical monsoon climate. The temperature varies between 24 and 29 °C, with an average of 26.2 °C. The precipitation is characterized by a wet and a dry season. The total annual precipitation amounts to 2400 mm. During the monsoon, large areas of the park under 130 m altitude are flooded (Vandekerkhove *et al.* 1993; Tordoff *et al.* 2004).

Cat Tien National Park supports a variety of habitat types, including primary and secondary lowland evergreen forest dominated by species in the Dipterocarpaceae; primary and secondary lowland semi-deciduous forest, dominated by *Lagerstroemia spp*. mixed with Fabaceae, Tetramelaceae, Rubiaceae, Datiscaceae, Ebenaceae, and some other families; freshwater wetlands with open lakes and seasonally inundated grasslands; flooded forest, dominated by *Hydnocarpus anthelmintica* mixed with *Ficus benjamina*; and a range of secondary habitat types, including grassland and areas dominated by bamboo (Vandekerkhove *et al.* 1993; Blanc *et al.* 2000; Tordoff *et al.*, 2004).

Morphological study

Specimens were photographed in the field, and their macromorphological characters, such as size, color, shape, and surface of all parts of the basidiomata as well as odor, were documented before drying. Color codes refer to Kornerup & Wanscher (1978). GPS coordinates of collection site, habitat, and substrate type were also documented for each collection. Specimens were then dried either in airtight plastic containers with silica gel, or with an electric dryer at a temperature ca. 50 °C, placed on a piece of absorbent paper and packed in plastic Ziploc bags with small amounts of silica gel.

Microscopic measurements and drawings were made with an AxioScope A1 light microscope equipped with Zeiss AxioCam 1Cc3 digital camera with AxioVisionRel.4.6 software (CarlZeiss, Germany). Spores, basidia, and cystidia were observed in squash preparations of small parts of the lamellae in 5 % KOH or 1 % Congo Red in concentrated NH_4OH. The pileipellis was examined from a radial section of the pileus in 5 % KOH. Basidiospore dimensions were based on 20 spores; cystidia and basidia dimensions on at least 10 structures per collection. Basidia were measured without sterigmata, and the spores without hilum. Spore length to width ratios were reported as Q.

The dried specimens were deposited in the Mycological Herbarium of the Komarov Botanical Institute RAS (LE) and in the Herbarium of the Joint Vietnam-Russian Tropical Research and Technological Centre, Hanoi (VRTC).

DNA extraction, amplification, and sequencing

DNA was extracted from herbarium material using NucleoSpin® Plant II (Macherey-Nagel, Germany). The ribosomal ITS1–5.8S–ITS2 region was amplified with the fungal specific primers ITS1F and ITS4B (Gardes & Bruns 1993; http://www.biology.duke.edu/fungi/mycolab/primers.htm). Sequences of nrLSU-rDNA were generated using primers LR0R and LR5 (Vilgalys & Hester 1990). PCR products were visualized using agarose gel electrophoresis and Gel Red staining, and subsequently purified with the Fermentas Genomic DNA Purification Kit (Thermo Fisher Scientific, MA, USA). Sequencing was performed with an ABI model 3500 Genetic Analyzer (Applied Biosystems, CA, USA). This work was carried out using equipment of Core Facility Centre 'Cell and Molecular Technologies in Plant Science' of the Komarov Botanical Institute. Raw data were edited and assembled in MEGA X (Kumar *et al.* 2018). Newly generated sequences have been deposited in the GenBank (Table 1).

Alignment and phylogenetic analyses

For this study, 11 nrITS and 5 nrLSU sequences were newly generated. In addition, 38 nrITS and 35 nrLSU sequences, including outgroups, were retrieved from the GenBank database (www.ncbi.nlm.nih.gov/genbank), using the BLASTn application (https:// blast.ncbi.nlm.nih.gov/Blast.cgi). Two datasets were analyzed: nrITS and nrLSU. The sequences were aligned with the Muscle tool incorporated into MEGA X program, and then manually modified where necessary in MEGA X (Kumar *et al.* 2018). To determine the phylogenetic positions of the studied collections, both datasets were analyzed using Bayesian Analysis (BA). BA was performed using MrBayes 3.2.1 (Ronquist *et al.* 2012), under a GTR model for LSU data set and GTR+G model for ITS. The analyses were run with two parallel searches, four chains for 5 million generations, starting with a random tree. The trees were sampled every 100 generations. To check for convergence of MCMC analyses and to get estimates of the posterior distribution of parameter values, Tracer v1.7.2 was used (Rambaut *et al.* 2018). The phylogenetic trees were edited in Adobe Illustrator CS4. Posterior probability (PP) values ≥0.95 are considered significant.

TABLE 1. Specimens and GenBank accession numbers of DNA sequences used in the molecular analyses.

Species	Location	Collection, voucher number	Genbank accession no.		References
			nrITS	nrLSU	
Entoloma abortivum	Russia: Far East	A. Kovalenko LE 312419	MF476905	MF487792	Morozova *et al*. (2018)
E. araneosum	Belgium	M.E. Noordeloos (MEN 200314)	KC710056	GQ289153	Co-David *et al*. (2009)
E. argus	Vietnam	O. Morozova (LE F-312694, holotype)	OM987263	OM996175	This study
E. argus	Vietnam	E. Popov (LE F-312695)	OM987262	—	This study
E. argus	Vietnam	O. Morozova (LE F-315915	OM987265	—	This study
E. argus	Vietnam	A. Alexandrova (LE F-315916)	OM987264	—	This study
E. arion	Vietnam	O. Morozova, E. Popov (LE F-312691, holotype)	OM987259	OM996176	This study
E. arion	Vietnam	O. Morozova, E. Popov (LE F-312692)	OM987260	—	This study
E. arion	Vietnam	O. Morozova, E. Popov (LE F-315917)	OM987261	—	This study
E. atricolor	Vietnam	O. Morozova, E. Popov (LE F-295000, holotype)	KY777496	KY777500	Morozova *et al*. (2018)
E. azureosquamulosum	China	X.-L. He (GDGM 27355)	NR_137086	JQ410325	He *et al*. (2012)
E. bidupense	Vietnam	E. Popov, O. Morozova (LE 262935, holotype)	MF476906	MF487793	Morozova *et al*. (2018)
E. byssisedum var. *byssisedum*	Spain	J. Vila (JVG 1080907-1)	KJ001413	—	Vila *et al*. (2014)
E. byssisedum var. *microsporum*	Russia: European part	O. Morozova (LE 311782)	ON329327	OM996178	This study
E. byssisedum var. *microsporum*	China	X.-L. He (SAAS1828)	KU312120	KU534234	He *et al*. (2019)
E. callidermum	Malaysia	Stubbe 06252 (GENT)	KC710115	KC710153	Morgado *et al*. (2013)
E. cetratum	Russia: European part	O. Morozova (LE 235480)	KC898450	MF487798	Morozova *et al*. (2014, 2018)
E. chalybeum	Russia: European part	E. Morozova (LE 254353)	KC898445	KC898500	Morozova *et al*. (2014)
E. chytrophilum	Spain: Canary Islands	R.M. Dähncke (L855, holotype)	KC898434	KC898519	Morozova *et al*. (2014)
E. clypeatum	The Netherlands	M.E. Noordeloos (MEN 198302)	KC710059	KC710136	Morgado *et al*. (2013)
E. conchatum	China	X.L. He (SAAS 1712, holotype; ZT 13628, isotype)	KU312111	KU534220	He *et al*. 2019
E. conferendum	Slovakia	M.E. Noordeloos (MEN 200330)	KC710055	KC710133	Morgado *et al*. (2013)
E. cyanostipitum	China	X.-L. He (GDGM 31318)	NR_154977	NG_059261	He e*t al*. (2017)
E. daphnis	Vietnam	A. Kovalenko (LE F-262915, holotype)	OM987266	OM996177	This study
E. ekaterinae	Russia: Far East	E. Malysheva (LE 312053, holotype)	NR_166276	MK733926	Crous *et al*. (2019)
E. erhardii	Russia: Caucasus	T. Svetasheva (LE 312051, holotype)	NR_166277	MK733924	Crous *et al*. (2019)

.....continued on the next page

TABLE 1. (Continued)

Species	Location	Collection, voucher number	Genbank accession no. nrITS	nrLSU	References
E. flabellatum	China	X.L. He (SAAS 1080, holotype; ZT 13612, isotype)	KU312115	KU534217	He *et al*. (2019)
E. flocculosum	Spain	J. Vila (JVG 1080920-20)	KJ001438	KJ001463	Vila *et al*. (2014)
E. gregarium	China	X.L. He (SAAS 1220, holotype)	KU312122	KU534237	He *et al*. (2019)
E. griseocyaneum	Russia: Caucasus	O. Morozova (LE 254351)	KC898444	KC898498	Morozova *et al*. (2014)
E. icarus	Vietnam	E. Popov (LE F-312696, holotype)	OM987257	OM996174	This study
E. icarus	Vietnam	E. Popov (LE F-312697)	OM987258	—	This study
E. kovalenkoi	Vietnam	E. Popov, O. Morozova (LE 312529, holotype)	OK257210	OK257207	Crous *et al*. (2021)
E. nigrovelutinum	Vietnam	A. Alexandrova (LE 295077, holotype)	NR_158429	MF898427	Crous *et al*. (2017)
E. nitidum	Slovakia	M.E. Noordeloos (MEN 200324)	KC710122	GQ289175	Co-David *et al*. (2009), Morgado *et al*. (2013)
E. pleurotoides	China	X.L. He (SAAS 1252, holotype; ZT 13610, isotype)	KU312113	KU534227	He *et al*. (2019)
E. quadratum	Russia: Far East	E. Malysheva (LE 254355)	KC898452	MF487800	Morozova *et al*. (2014, 2018)
E. reductum	China	(SAAS 1091, holotype; ZT 13607, isotype)	KU312123	KU534232	He *et al*. (2019)
E. rusticoides	Spain	J. Vila (LIP JVG 1020416U, epitype)	KJ001434	KJ001478	Vila *et al*. (2014)
E. serrulatum	Russia: Caucasus	O. Morozova (LE 254361)	KC898447	KC898501	Morozova *et al*. (2014)
E. sinuatum	Finland	J. Vauras 8181F (TUR)	KC710116	KC710154	Morgado *et al*. (2013)
E. subcaesiellum	Russia: Far East	O. Morozova (LE 253776, holotype)	NR_164610	—	Crous *et al*. (2019)
E. subcaesiocinctum	China	X.-L. He (SAAS 133, holotype)	NR_155101	NG_059262	He *et al*. 2017
E. turbidum	Slovakia	M.E. Noordeloos (MEN 200351)	KC710060	GQ289201	Co-David *et al*. (2009), Morgado *et al*. (2013)
E. undatum	Russia: European part	O. Morozova (LE 312417)	MF476910	MF487801	Morozova *et al*. (2018)
E. vernum	Russia: European part	S. Arslanov (LE 312418)	MF476911	MF487802	Morozova *et al*. (2018)
E. violaceoserrulatum	Finland	J. Vauras (JV8329F, isotype (TUR))	MF476913	MF487803	Morozova *et al*. (2018)

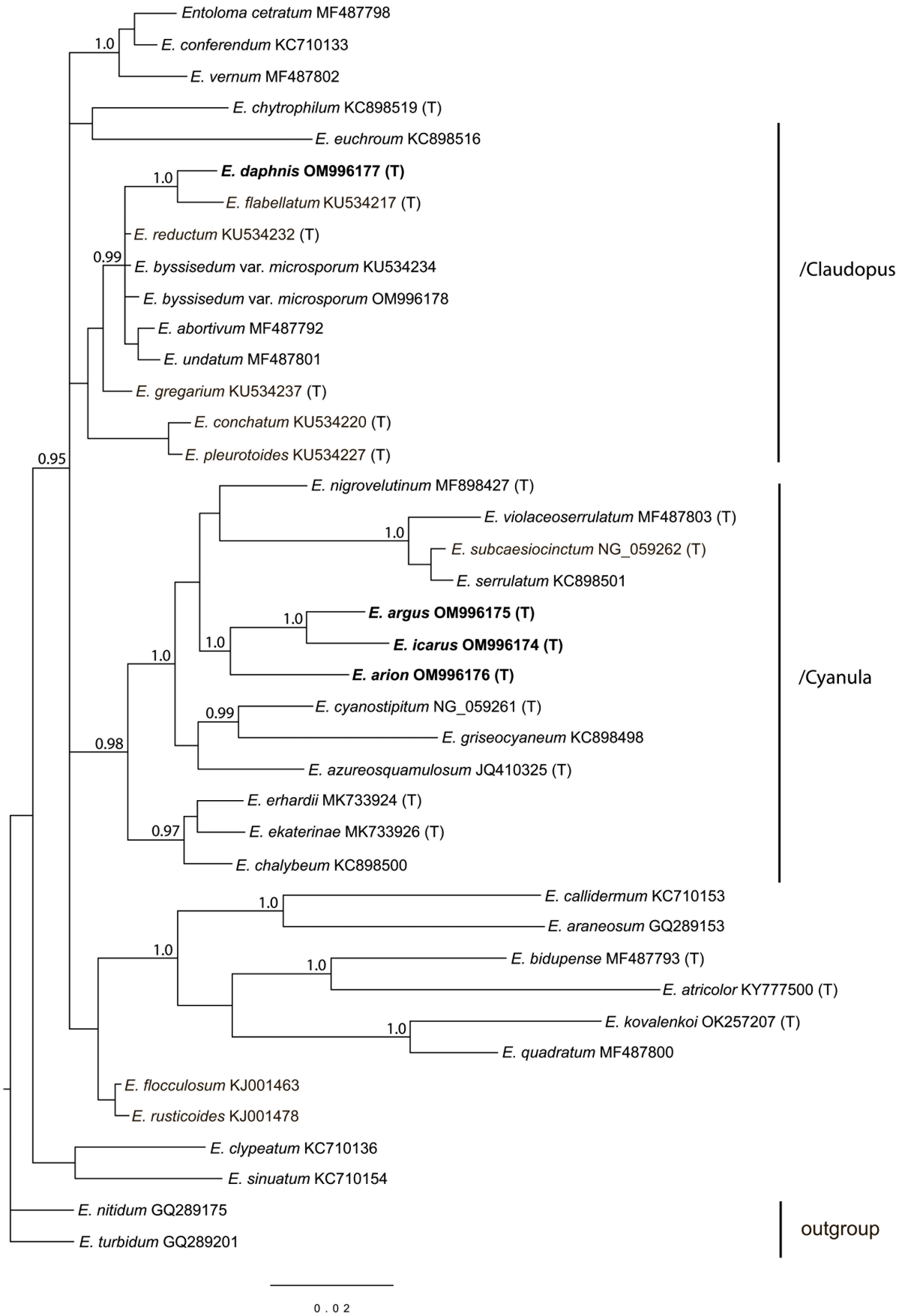

FIGURE 1. Phylogenetic tree derived from Bayesian analysis, based on nrLSU data. Posterior probability (PP > 0.95) values from the Bayesian analysis are added at the nodes. The scale bar represents the number of nucleotide changes per site. (T) indicates the type specimen for this species. The new species are in bold.

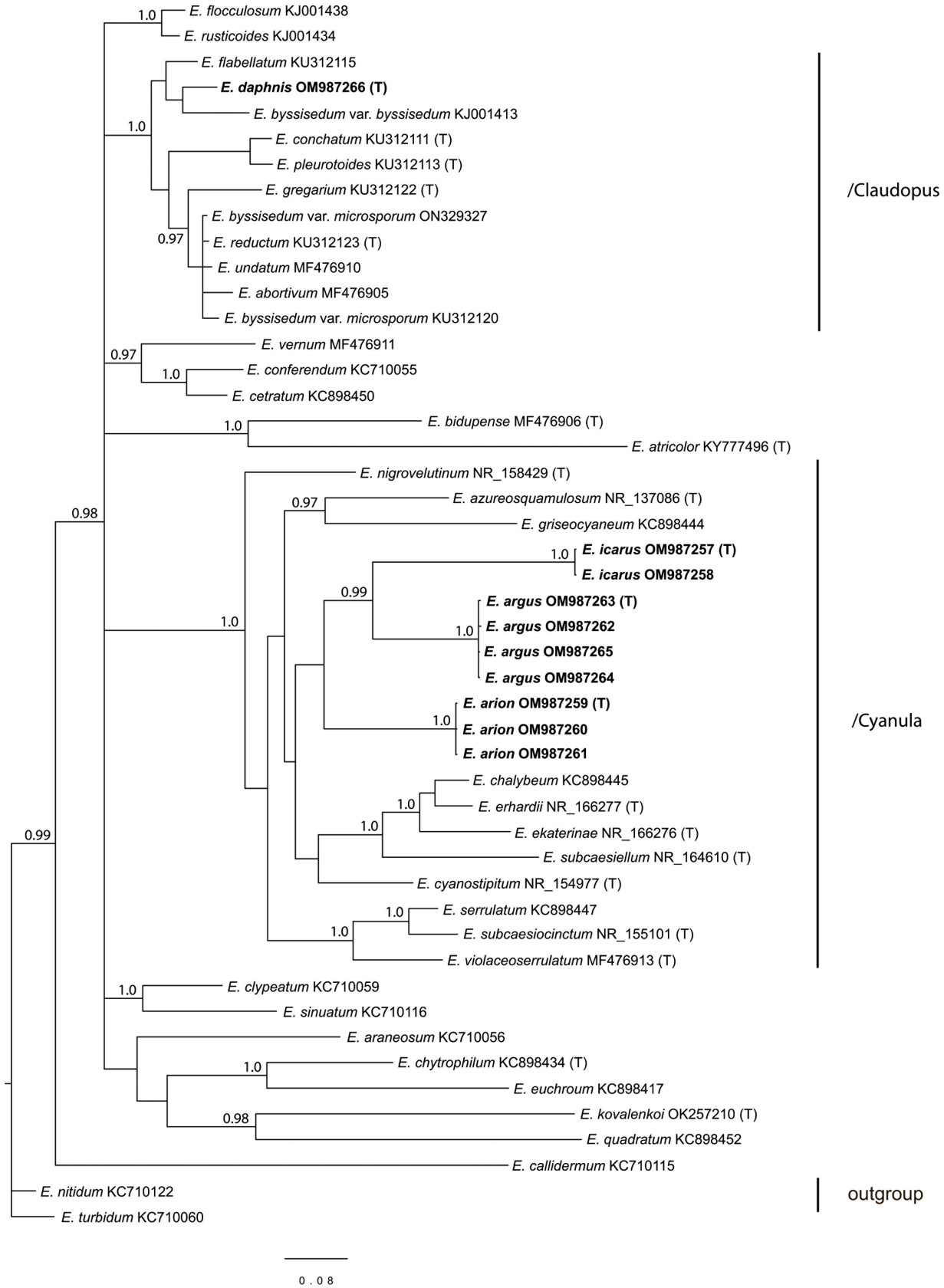

FIGURE 2. Phylogenetic tree derived from Bayesian analysis, based on nrITS1-5.8S-ITS2 region data. Posterior probability (PP > 0.95) values from the Bayesian analysis are added at the nodes. The scale bar represents the number of nucleotide changes per site. (T) indicates the type specimen for this species. The new species are in bold.

Results

Phylogenetic analysis

The full LSU dataset contained 40 sequences with 761 characters, and the ITS dataset contained 48 sequences with 829 characters (gaps included). The /Entocybe clade was selected as outgroup for both trees due to its basal position in the *Entoloma* phylogeny (Baroni *et al.* 2011). The trees include 9 and 10 representatives of subgenera *Claudopus* and *Cyanula*, and 1–3 representatives of the other main subdivisions of the *Entoloma s.l.* (subgen. *Nolanea*, subgen. *Rhodopolia*, subgen. *Pouzarella*, subgen. *Leptonia*, subgen. *Cubospora*, sect. *Calliderma, Rusticoides*-group). The trees have nearly similar topology. In the ITS tree all the subgenera clades are well-supported, in the LSU tree not all these clades received such support. However, in both trees three of the new species (*Entoloma argus*, *E. arion*, and *E. icarus*) are clustered together and belong to subgenus *Cyanula* (*i.e.*, /Cyanula clade). *Entoloma daphnis* is placed within subgenus *Claudopus* (*i.e.*, the /Claudopus clade) in the LSU tree, close to the recently described *E. flabellatum* Xiao L. He & E. Horak, in He *et al.* (2019: 8) from China, and in the ITS tree it groups with a Spanish collection of *E. byssisedum*. According to recent molecular data, the morphospecies *E. byssisedum* represents a complex of different and phylogenetically distant species (He *et al.* 2019).

Our molecular studies confirmed the assumption based on morphological analysis that three of the new species belong to the subgenus *Cyanula*, including one species with pleurotoid basidiocarps (*E. icarus*). Another pleurotoid taxon initially identified as *Entoloma nubilum* (Morozova *et al.* 2012) is nested within the /Claudopus clade. Revision of this collection revealed several morphological differences between our species and *E. nubilum*, so the decision was made to describe it as a new species, *E. daphnis*.

Taxonomy

Entoloma* subgenus *Cyanula (Romagn.) Noordel., in Noordeloos & Gates, Entolomataceae of Tasmania (Hong Kong): 209 (2012)

Entoloma argus O.V. Morozova, E.S. Popov, A.V. Alexandrova & Noordeloos, *sp. nov*. (Figs. 3, 4)

Mycobank: MB 843250

Type:—VIETNAM. Gia Lai Province, K'Bang District, Son Lang Commune, Kon Chu Rang Nature Reserve, N 14.505520°, E 108.541610°, 1050 m a.s.l., on soil in middle-mountain evergreen mixed forest with a predominance of Podocarpaceae (*Dacrydium elatum, Dacrycarpus imbricatus*), Magnoliaceae, Burseraceae (*Canarium*), Myrtaceae (*Syzygium*), 26 May 2016, *O.V. Morozova* (holotype: LE F-312694 (!), isotype in VRTC (!), ITS sequence GenBank OM987263, LSU sequence GenBank OM996175).

Etymology:—Ἄργος (Greek), Argus (Lat.) a character from ancient Greek mythology. Argos was a one hundred-eyed giant who paid a service to the goddess Hera. Zeus killed the giant, but Hera remembered the giant by placing his one hundred eyes on the tail of the peacock. His name is used in various combinations in the generic and species names of butterflies of the Lycaenidae (Cupidinidae) family. The new *Entoloma* species is named after the butterfly *Plebejus argus*, due to the similarity of color.

Diagnosis:—*Entoloma argus* is characterized by the delicate greyish blue basidiomata with the distinctly translucently striate pileus covered by small dark blue squamules on a paler greyish blue background with contrasting dark blue centre, and the smooth, polished stipe concolorous with pileus. Microscopically, the sterile lamella edge of cylindrical to narrowly clavate colorless cystidia, and rather small 5–6 angled spores are characteristic.

Description:—*Basidiomata* small to medium-sized, collybioid. *Pileus* 15–25 mm diam., hemispherical to convex soon expanding to plano-convex with flat to slightly depressed centre, with deflexed then straight margin, hygrophanous, translucently striate almost up to the centre, greyish blue (21C–D4–7), covered with dark blue squamules, glabrescent with age and discoloring to greyish beige, with dark blue (21F6–8) fibrillose center. *Lamellae* moderately distant, adnate-emarginate, ventricose, white, becoming pinkish, with entire edge concolorous with faces. *Stipe* 30–60 × 1–1.5 mm, cylindrical, smooth, polished, greyish blue, concolorous with pileus (21C–D4–7), with white tomentum at base. *Context* white, greyish under the surface. *Smell* indistinct, *taste* not reported.

Basidiospores (8.5–)9.5–10(–11.4) × (6.0–)6.5–7(–7.5) µm, Q = (1.3–)1.45–1.5(–1.6), heterodiametrical, with 5–6 angles in side-view. *Basidia* 24–34 × 8.5–11.5 µm, 1–2-spored or 4-spored, narrowly clavate to clavate, clampless. *Cheilocystidia* 33–53 × 7.5–14 µm, cylindrical to narrowly clavate, sometimes septate, not pigmented, forming a sterile lamellae edge. *Pileipellis* a cutis of cylindrical hyphae 2–7 µm diam with trichodermal bundles of ascending hyphae

with cylindrical to narrowly clavate terminal elements (46–86 × 14–20 µm) forming the macroscopic squamules and central disk of pileus. Clamp connections absent.

Habitat and distribution:—In small groups in middle-mountain evergreen mixed forests. Known from Vietnam.

Additional specimens examined:—VIETNAM. Gia Lai Province, K'Bang District, Son Lang Commune, Kon Chu Rang Nature Reserve, on soil in middle-mountain evergreen mixed forest with a predominance of Podocarpaceae (*Dacrydium elatum*, *Dacrycarpus imbricatus*), Magnoliaceae, Burseraceae (*Canarium*), Myrtaceae (*Syzygium*), path to the waterfall, N 14.51361°, E 108.54621°, 1007 m a.s.l., 25 May 2016, *A. Alexandrova* (LE F-315916 (!), ITS sequence GenBank OM987264); ibid., N 14.505520°, E 108.541610°, 1050 m a.s.l., 28 May 2016, *I. Semenyuk* and *E. Popov* (LE F-312695 (!), ITS sequence GenBank OM987262); ibid., on the river bank, 28 May 2016, *O.V. Morozova* (LE F-315915 (!), ITS sequence GenBank OM987265).

FIGURE 3. *Entoloma argus*: a–c. basidiocarps; d. basidiospores; e. cheilocystidia; f. pileipellis (a, d–f, from LE F-312694, holotype; b–c, from LE F-315915). Scale bars a–c 1 cm, d–f 10 µm. Photos by O. Morozova.

Notes:—*Entoloma argus* is distinguished from the macromorphologically similar *E. ekaterinae* O.V. Morozova, Noordel., K. Nara, Dima & Brandrud, in Crous *et al.* (2019: 413) from the Russian Far East by the more applanate pileus, different pileipellis structure and shape of the cheilocystidia (cylindrical *vs*. broadly clavate and subglobose). *E. subcaesiellum* Noordeloos & O.V. Morozova (2010: 243) also described from the Russian Far East possesses a less squamulose pileus with blue squamules on a greyish beige background and microscopically lacks a distinct trichoderm at pileal center. The European *E. phaeodiscum* Vila & F. Caballero (2007: 41) differs by the absence of cheilocystidia, less pronounced, fading blue coloration, and geographical distribution.

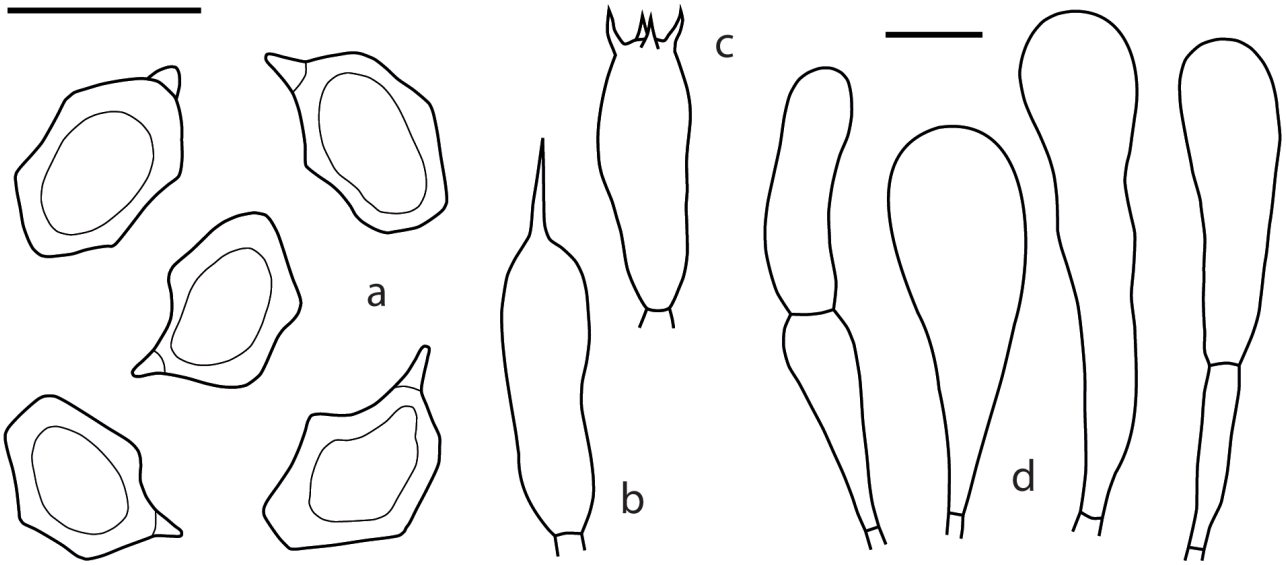

FIGURE 4. *Entoloma argus*: a. basidiospores; b, c. basidia; d. cheilocystidia (a, b, d, from LE F-312694, holotype; c, from LE F-315915). Scale bars 10 μm. Drawings by O. Morozova.

Entoloma arion O.V. Morozova, E.S. Popov, T.H.G. Pham & Noordeloos, *sp. nov*. (Figs. 5, 6)

Mycobank: MB 843251

Type:—VIETNAM. Gia Lai Province, K'Bang District, Son Lang Commune, Kon Chu Rang Nature Reserve, N 14.487996°, E 108.57101°, 960 m a.s.l., on soil along a track in middle-mountain evergreen mixed forest with a predominance of Podocarpaceae (*Dacrydium elatum, Dacrycarpus imbricatus*), Magnoliaceae, Burseraceae (*Canarium*), Myrtaceae (*Syzygium*), 29 May 2016, *O.V. Morozova* and *E.S. Popov* (holotype: LE F-312691 (!), isotype in VRTC (!), ITS sequence GenBank OM987259, LSU sequence GenBank OM996176).

Etymology:—Ἀρίων (Greek), Arion (Lat.) a Greek poet, singer and musician who played the cithara (7–6th centuries BC). According to legend, Arion sailed with rich treasures on a ship to Corinth. The sailors, wanting to take possession of the singer's wealth, threw him overboard, but Arion was rescued by a dolphin and safely reached Corinth. A butterfly *Phengaris arion* of the Lycaenidae (Cupidinidae) family with a blue upper and a light under surface of the wings was named after him. Our new species is similar to it in colors.

Diagnosis:—*Entoloma arion* is characterized by the bright blue, radially fibrillose pileus with rather dark blue central spot and scales at first densely covering whole surface, moving apart with pileus expansion, showing a whitish or light blue background, and a white stipe that is minutely innately fibrillose and pruinose at the apex. Microscopically, cylindrical to broadly clavate septate cheilocystidia and caulocystidia in the form of bundles of long hairs are distinctive.

Description:—*Basidiomata* small to medium-sized, collybioid. *Pileus* 10–25 mm diam., hemisphaerical, convex, soon expanding to plano-convex with flat to slightly depressed centre, with deflexed then straight margin, non hygrophanous, non translucently striate, radially fibrillose, at first entirely densely covered with dark blue to blackish blue squamules (20E–F6–8), moving apart with pileus expansion showing whitish or light blue (20B–C4–6) background, with fibrillose, contrasting blackish blue centre. *Lamellae* moderately distant, broadly adnate, slightly emarginate with a small tooth, segmentiform to arcuate, white, or pale bluish in young basidiomata, becoming pinkish, with irregular concolorous edge. *Stipe* 30–70 × 1.5–2 mm, cylindrical, minutely innately fibrillose, pruinose in upper part, translucent, white or pale bluish in young basidiomata. *Context* white. *Smell* indistinct, *taste* not reported.

Basidiospores (9.5–)10.5–12(–13) × (6.5–)7–7.5(–8.5) μm, Q = (1.3–)1.5(–1.7), heterodiametrical, with 5–6

angles in side-view. *Basidia* 23–30 × 9–12 µm, 1–2-or 4-spored, narrowly clavate to clavate, clampless. *Cheilocystidia* 27–78 × 7–18 µm, cylindrical or narrowly to broadly clavate, often septate, not pigmented, forming a sterile lamellar edge or intermixed with basidia. *Pileipellis* a cutis with transition to a trichoderm, composed of repent cylindrical hyphae 4–8 µm diam with narrowly clavate to fusoid ascending terminal elements 70–210 × 15–25 µm, a trichoderm at center. *Caulocystidia* in the form of bundles of hairs up to 200 µm long composed of chains of cylindrical cells 23–44 × 5–10 µm. Clamp connections absent.

FIGURE 5. *Entoloma arion*: a–c. basidiocarps; d. cheilocystidia; e. basidiospores; f. pileipellis; g. caulocystidia (all from LE F-312691, holotype). Scale bars a–c 1 cm, d–g 10 µm. Photos by O. Morozova.

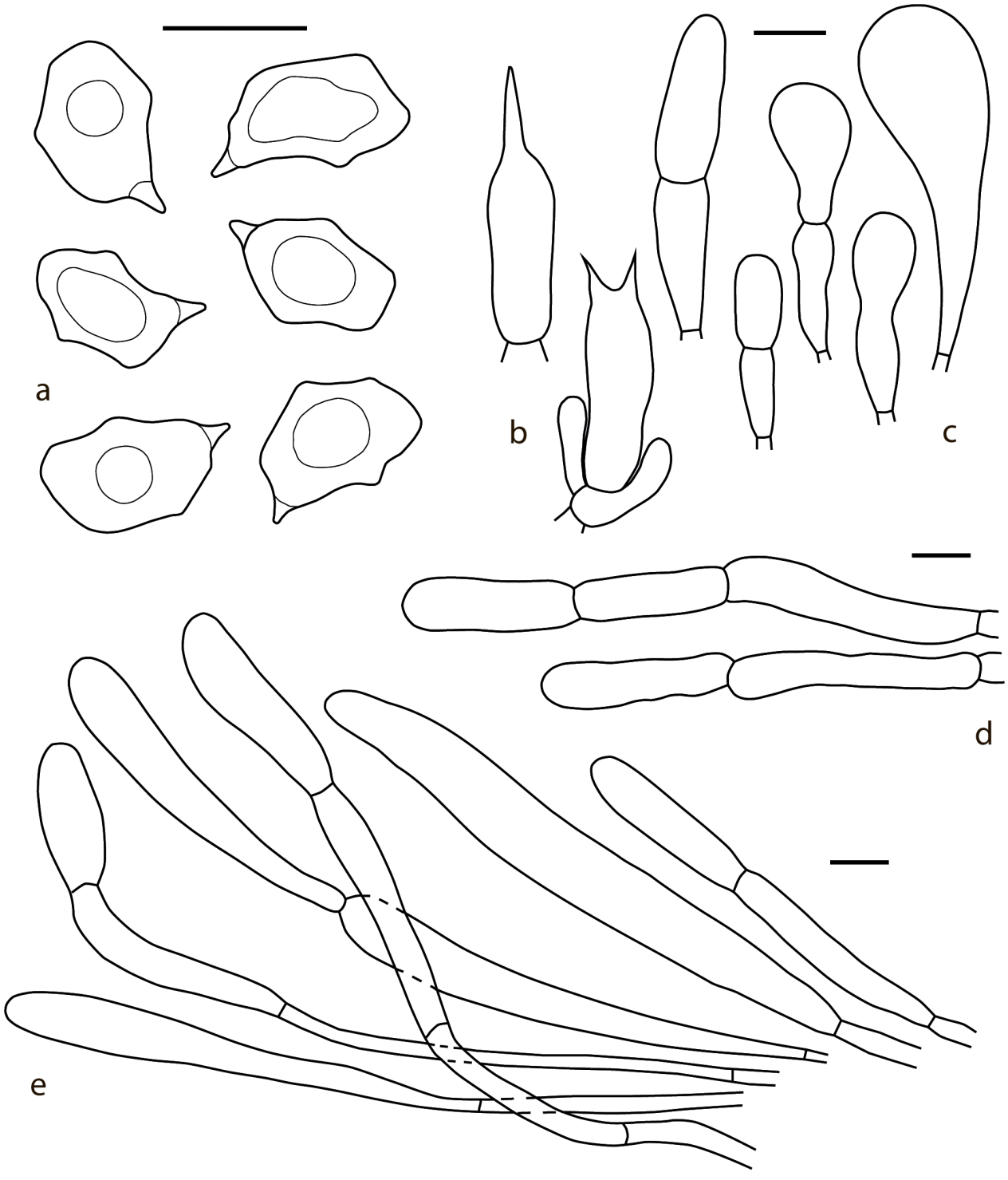

FIGURE 6. *Entoloma arion*: a. basidiospores; b. basidia; c. cheilocystidia; d. caulocystidia; e. pileipellis (all from LE F-312691, holotype). Scale bars 10 μm. Drawings by O. Morozova.

Habitat and distribution:—In small groups in the middle-mountain evergreen mixed forests. Known only from Vietnam.

Additional specimens examined:—VIETNAM. Gia Lai Province, K'Bang District, Son Lang Commune, Kon Chu Rang Nature Reserve, N 14.49776°, E 108.556993°, 975 m a.s.l., on soil along a track in middle-mountain evergreen mixed forest with a predominance of Podocarpaceae (*Dacrydium elatum, Dacrycarpus imbricatus*), Magnoliaceae, Burseraceae (*Canarium*), Myrtaceae (*Syzygium*), 28 May 2016, *O.V. Morozova* and *E.S. Popov* (LE F-312692 (!), ITS sequence GenBank OM987260; LE F-315917 (!), ITS sequence GenBank OM987261).

Notes:—*Entoloma arion* can be easily recognized by the bright blue pileus and contrasting white stipe, a very rare combination in subgenus *Cyanula*. *Entoloma floccosodentatum* Corner & E. Horak, in Horak (1980: 288) from New Caledonia is superficially similar in colors, spore size and cystidia form, but its pileus is pale blue and smooth, or only innately fibrillose, or tomentose. The presence of clamps on the hyphae indicates that *Entoloma floccosodentatum* does not belong to the subgenus *Cyanula*. Geographically it is also very distant and isolated.

Entoloma icarus O.V. Morozova, E.S. Popov & Noordeloos, *sp. nov*. (Figs. 7, 8)
Mycobank: MB 843252

FIGURE 7. *Entoloma icarus*: a–c. basidiocarps; d. basidiospores; e. cheilocystidia; f. pileipellis (all from LE F-312696, holotype). Scale bars a–c 1 cm, d–f 10 µm. Photos a by E. Popov, b–f by O. Morozova.

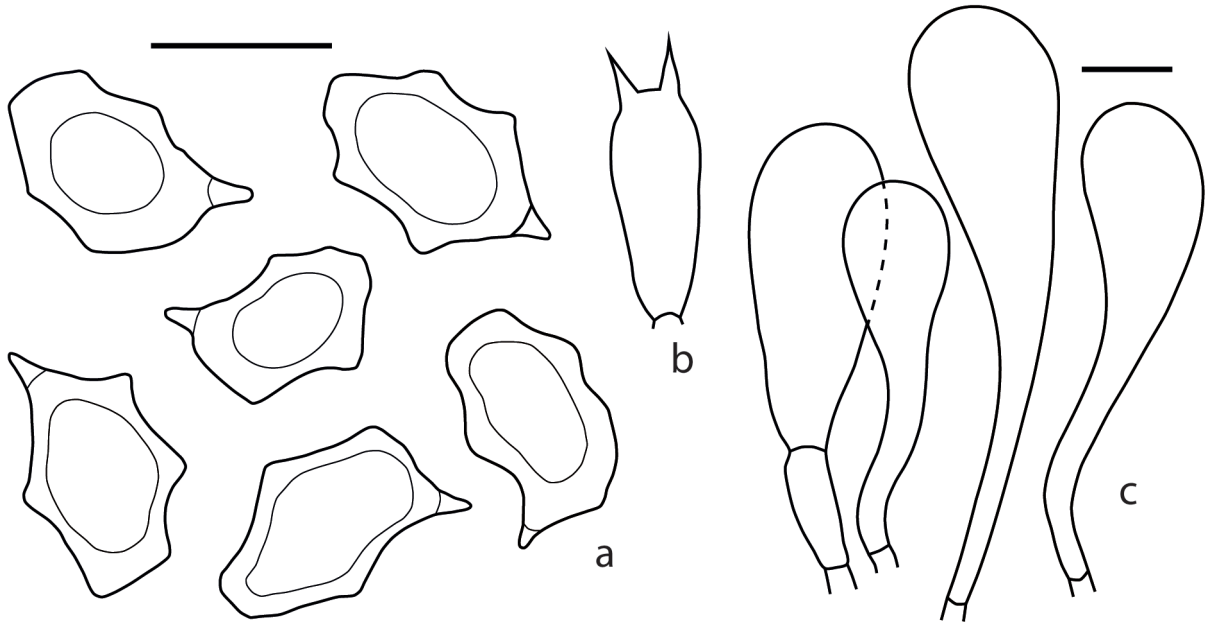

FIGURE 8. *Entoloma icarus*: a. basidiospores; b. basidium; c. cheilocystidia (all from LE F-312696, holotype). Scale bars 10 μm. Drawings by O. Morozova.

Type:—VIETNAM. Gia Lai Province, K'Bang District, Son Lang Commune, Kon Chu Rang Nature Reserve, near the camp, N 14.505520°, E 108.541610°, 1050 m a.s.l., on decaying wood in middle-mountain evergreen mixed forest with a predominance of Podocarpaceae (*Dacrydium elatum*, *Dacrycarpus imbricatus*), Magnoliaceae, Burseraceae (*Canarium*), Myrtaceae (*Syzygium*), 26 May 2016, *E. Popov* (holotype: LE F-312696 (!), isotype in VRTC (!), ITS sequence GenBank OM987257, LSU sequence GenBank OM996174).

Etymology:—Ἴκαρος (Greek), Îcărus (Lat.) in Greek mythology, was the son of the master Daedalus, the creator of the Labyrinth. Icarus and Daedalus attempted to escape from Crete by means of wings that Daedalus had constructed from feathers and wax. Icarus ignored his father's instructions not to fly too close to the sun, and the wax in his wings melted. He fell out of the sky into the sea and drowned. The butterfly *Polyommatus icarus* was named after him. The new *Entoloma* species is named after this butterfly, due to the similarity of color.

Diagnosis:—*Entoloma icarus* is characterized by the eccentrically stipitate to pleurotoid basidiomata with a minutely squamulose blue pileus and whitish or blue-tinged short stipe, the initially uniformly colored pileus, which becomes distinctly translucently striate with small blue squamules on a paler greyish beige background with age. Microscopically, the rather large spores and sterile lamellar edge composed of cylindrical to narrowly clavate cystidia are characteristic.

Description: *Basidiomata* small to medium-sized, pleurotoid or with eccentric stipe. *Pileus* 10–25 mm diam., hemisphaerical to convex soon expanding to plano-convex with flat to slightly depressed centre, eccentric, with deflexed then straight margin, hygrophanous, translucently striate to half the radius, becoming sulcate with age, firstly radially fibrillose, greyish blue to dull or deep blue (21D–F5–7), then covered with dark blue squamules on a bluish or brownish grey background (20C–D2–3, 6C–D2–3), more dense at first becoming sparse, discoloring to brownish grey with bluish pileus margin. *Lamellae* moderately distant, adnate-emarginate, ventricose, whitish with or without bluish tinge, becoming pinkish, with entire blue edge. *Stipe* 5–10 × 1–1.5 mm, lateral, cylindrical, slightly innately fibrillose, pubescent, whitish or bluish, with white tomentum at base. *Context* greyish. *Smell* indistinct, *taste* not reported.

Basidiospores (10–)11.8–12(–13.3) × (7.2–)8(–9) μm, Q = (1.4–)1.5(–1.6), heterodiametrical, with 5–7 rather sharp angles in side-view. *Basidia* 24–30 × 9–10.5 μm, 2–4-spored, narrowly clavate, clampless. *Cheilocystidia* 33–53 × 7.5–14 μm, cylindrical to narrowly clavate, sometimes septate, non pigmented, forming a sterile lamellar edge. *Pileipellis* a cutis of cylindrical hyphae 2–7 μm diam with ascending cylindrical to narrowly clavate terminal elements (45–90 × 10–17 μm), that macroscopically form the squamules. Clamp connections absent.

Habitat and distribution:—In small groups on wood in the middle-mountain evergreen mixed forests. Known only from Vietnam.

Additional specimens examined:—VIETNAM. Gia Lai Province, K'Bang District, Son Lang Commune, Kon Chu Rang Nature Reserve, near the camp, N 14.505520°, E 108.541610°, 1050 m a.s.l., on decaying wood in

middle-mountain evergreen mixed forest with a predominance of Podocarpaceae (*Dacrydium elatum, Dacrycarpus imbricatus*), Magnoliaceae, Burseraceae (*Canarium*), Myrtaceae (*Syzygium*), 26 May 2016, *E. Popov* (LE F-312697 (!), ITS sequence GenBank OM987258).

Notes:—*Entoloma nubilum* Manim., Leelav. & Noordel. described from India differs by the non hygrophanous, non translucent-striate pileus, smaller spores and absence of cheilocystidia (Manimohan *et al.* 2002). *Entoloma cyanomelaenum* known only from the type locality in Sumatra possesses smaller spores (9–11 × 5.5–6.5 µm), lacks cystidia and the pileus turns red in KOH (Boedijn 1929; Horak 1980). *Entoloma gainsvillae* Morgan-Jones (1971: 1052) (=*E. cyaneum* (Murrill 1943: 429) Hesler (1967: 13) [non *E. cyaneum* (Peck 1873: 49) Saccardo (1887: 688)]) from Florida differs by smaller spores (8–10 × 6–7 µm) and lack of cheilocystidia (Murrill 1943; Hesler 1967; Morgan-Jones 1971).

Entoloma* subgenus *Claudopus (Gillet) Noordeloos, Persoonia 11: 147 (1981)

Entoloma daphnis O.V. Morozova, Kovalenko, E.S. Popov & Noordeloos, *sp. nov*. (Figs. 9, 10)

Mycobank: MB 843253

Type:—VIETNAM. Dong Nai Prov., Tan Phu Dist., Cat Tien National Park, "Lagerstroemia trail" near the Park's Headquarters, N 11.426667°, E 107.426389°, 125 m a.s.l., on fallen log in lowland semi-deciduous tropical forest, 14 June 2010, *A. Kovalenko* (holotype: LE F-262915 (!), as *Entoloma nubilum* in Morozova *et al.* 2012, ITS sequence GenBank OM987266, LSU sequence GenBank OM996177).

Etymology:—Δάφνις, from δάφνη–laurel (Greek), in Greek mythology, a beautiful young shepherd in Sicily and inventor of pastoral songs, the son of Hermes (Mercury). The butterfly *Polyommatus daphnis* was named after him. The new *Entoloma* species is named after this butterfly, due to the similar color.

Diagnosis:—*Entoloma daphnis* is characterized by small pleurotoid basidiomata, small spores with up to the 8 angles, a trichodermal pileipellis (pileus is densely covered by dark blue fibrils) and lack of cheilocystidia.

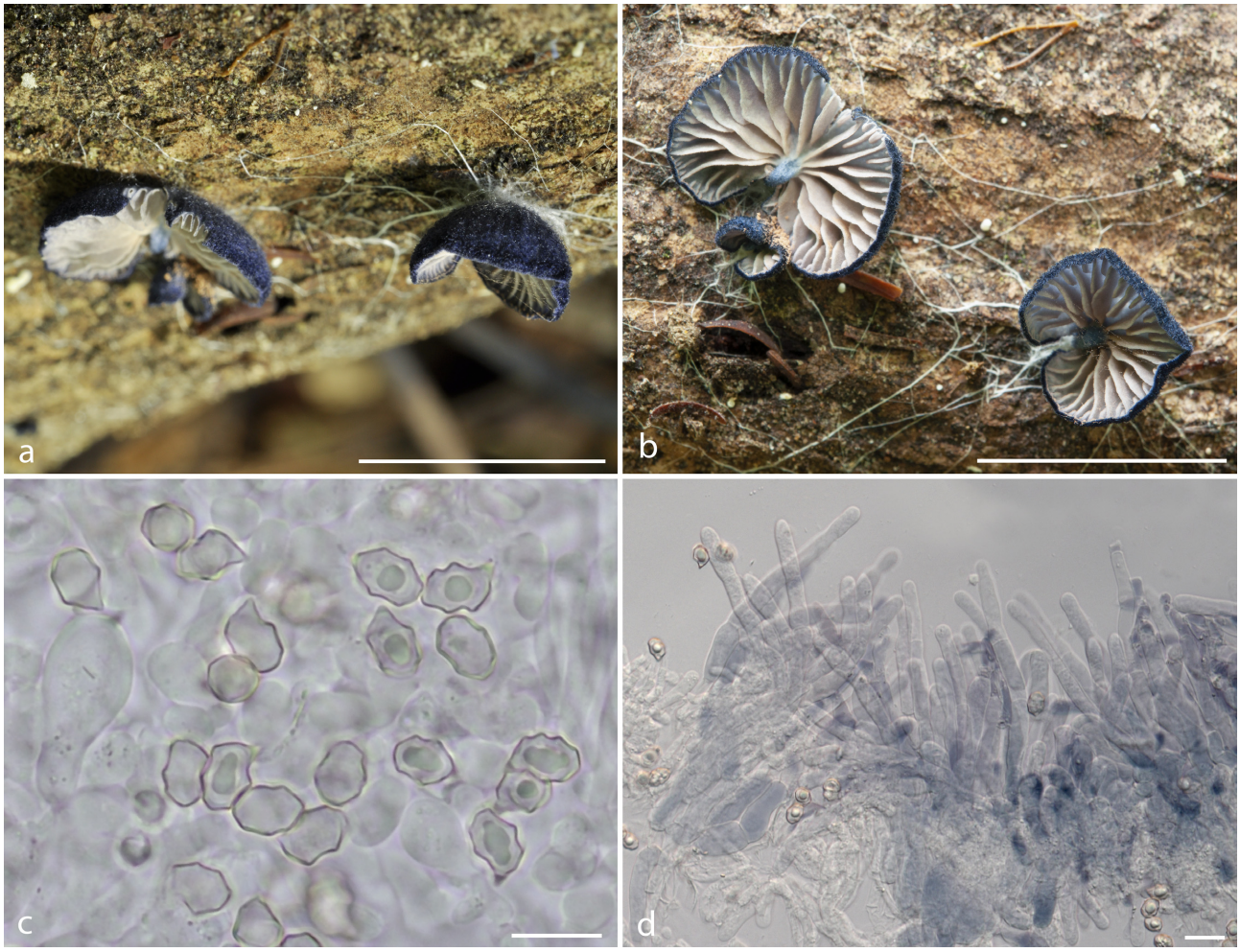

FIGURE 9. *Entoloma daphnis*: a–b. basidiocarps, c. basidiospores; d. pileipellis (all from LE F-262915, holotype). Scale bars a–b 1 cm, c–d 10 µm. Photos a–b by A. Kovalenko, c–d by O. Morozova.

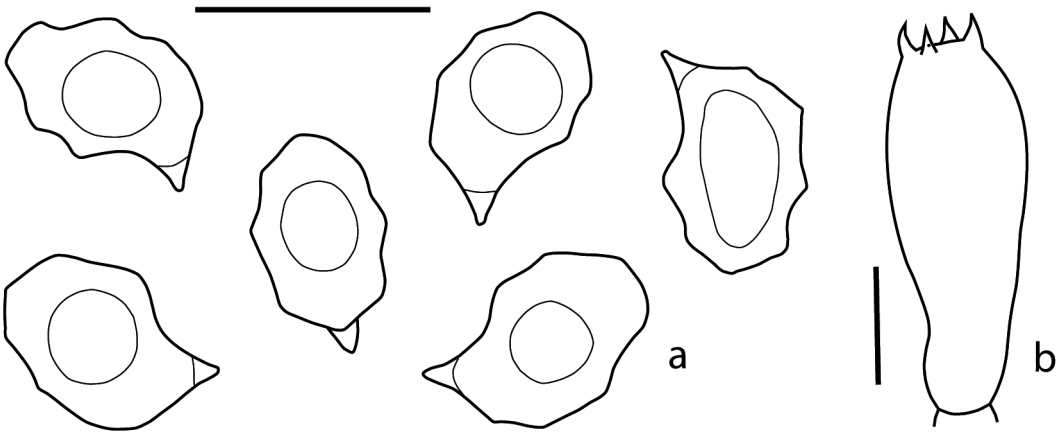

FIGURE 10. *Entoloma daphnis*: a. basidiospores; b. basidium (all from LE F-262915, holotype). Scale 10 μm. Drawings by O. Morozova.

Description:—*Basidiomata* small, pleurotoid. *Pileus* 3–7 mm diam., cupulate then reniform with incurved then lobate margin, non hygrophanous, slightly translucently striate, tomentose to finely squamulose, deep blue to dark blue (20D8, 20E7–8). *Lamellae* moderately distant intermixed with lamellulae, adnate or slightly emarginate, whitish to bluish near the pileal margin then pinkish with concolorous entire edge. *Stipe* 3–4 × 0.5–1 mm, reduced, eccentric or lateral, curved, pruinose to tomentose, concolorous with the pileus or slightly paler (20D7), with white arachnoid mycelial strands at the base attached to the substratum. *Context* thin, bluish, under the surface dark blue. *Odor* indistinct, *taste* not reported.

Basidiospores (7–)8.3(–9) × (5.5–)5.7(–6) μm, Q = (1.3–)1.45(–1.6), heterodiametrical, with 6–8 angles in side-view. *Basidia* 23–31 × 9–12 μm, clavate, clampless. *Lamellae edge* fertile. *Cheilocystidia* and *pleurocystidia* absent. *Pileipellis* a trichoderm of long hairs, composed of chains of cylindrical cells narrower at the apical part (27–62 × 5.5–6.5 μm), broader at the base (27–62 × 5.5–6.5 μm) with dark blue intracellular pigment. *Clamp connections*, *oleiferous hyphae* and *brilliant granules* absent.

Notes:—*Entoloma cyanomelaenum* possesses larger (9–11 × 5.5–6.5 μm) spores and its pileus turns red in KOH (Boedijn 1929; Horak 1980); *E. gainsvillae* has slightly larger spores (8–10 × 6–7 μm) and a smooth pileus (Murrill 1943; Hesler 1967); *E. nubilum* differs from *E. daphnis* by differently-shaped (5–7 angled) spores, a cutis-type pileipellis, and habitat on decaying leaves or on humus (Manimohan *et al.* 2002); *E. icarus* possesses larger (10–13 × 7–9 μm) differently-shaped (with 5–7 sharp angles) spores and cheilocystidia.

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