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Taxonomic revision of Stemonitidaceae (Stemonitidales, Myxomycetes) based on morphology and phylogeny: new genera, species, and combinations

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Abstract

Stemonitidales represents one of the most morphologically complex groups within Myxomycetes. While its monophyly is well-supported, phylogenetic relationships within Stemonitidales, particularly among members of Stemonitidaceae, remain poorly resolved. Extensive overlap in macromorphological and microstructural characteristics has resulted in ambiguous generic boundaries and inconsistent taxonomic criteria, complicating reliable species identification. Focusing on the genera *Stemonitis*, *Stemonaria*, *Stemonitopsis*, *Symphytocarpus*, and *Valtocarpus* within Stemonitidaceae, and including *Amaurochaete*, this study constructed a comprehensive phylogeny of Stemonitidales using 735 sequences (from 355 specimens) of nuclear small subunit ribosomal RNA, elongation factor-1 alpha, and mitochondrial small subunit ribosomal RNA genes. Analyses employed both Maximum Likelihood, with branch support assessed via Transfer bootstrap expectation to mitigate the impact of rogue taxa on the phylogenetic tree topology, and Bayesian inference methods. Detailed morphological studies, utilizing light and scanning electron microscopy, were performed on 290 collections from Belarus, Brazil, China, Japan, Nepal, Russia, the USA, and Vietnam. These collections included 13 type specimens from herbaria TNS and LE, alongside the designated lectotype of *Stemonitis splendens*. The results demonstrate that spore ornamentation is the most informative and stable characteristic for generic delimitation within Stemonitidaceae, specifically the *Stemonitis* s.l. complex, whereas the completeness of the surface net is unsuitable as a primary generic criterion in this group, although it remains useful at the species level. Combined morphological and phylogenetic evidence supports the establishment of two new genera: *Corallosporopsis,* characterized by bacula with apically thickened tips in spore ornamentation, and *Grandiverruca,* characterized by large and irregular verrucae. This research also presents an emended circumscription for *Stemonitis* (restricted to taxa with a simple reticulate ornamentation with perforated muri), *Stemonitopsis* (restricted to taxa with reticulated spores with irregular-sized meshes and low ridges), and *Symphytocarpus* (restricted to taxa with warted spores with barely visible to fine secondary ornamentation). Within this revised framework, 13 new species are described, two previously synonymized species (*Stemonitis castillensis* and *Stemonitis emotoi*) are resurrected, three basionyms are reinstated to replace currently accepted combinations, and 29 new combinations and one replacement name are proposed. Among these 30 taxonomic updates, six are supported by molecular data, while 24 are inferred solely from morphology. These updates provide new insights into the phylogeny and classification of this group.

Keywords: Amoebozoa, Dark-spored myxomycetes, Nomenclature, Phylogenetics, Slime-molds, Species complex, Taxonomy, 2 new genera, 13 new species, 29 new combinations, 1 replacement name, 1 lectotypification

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Introduction

Myxomycetes G. Winter constitute a monophyletic group within Amoebozoa Lühe[1–5]. As one of the most species-rich and widespread clades in Amoebozoa, they encompass over 1,200 described species[6] and inhabit nearly all terrestrial ecosystems globally[7,8], often being classified as a distinct group of fungus-like protists[9,10] which, together with dictyostelids, constitute the two primary lineages of slime molds[11]. Myxomycetes possess a complex life cycle comprising four distinct morphological stages: myxamoebae and swarm cells, plasmodia, sclerotia and microsclerotia, and spore-bearing sporocarps[12].

Traditional classification systems, which were based on sporocarp characteristics and divided the class Myxomycetes into three subclasses and six orders[13], have been significantly revised following recent advances in molecular phylogenetics. It is now widely accepted that Myxomycetes comprise two main lineages[4]: Lucisporomycetidae Leontyev, Schnittler, S.L. Stephenson, Novozhilov & Shchepin (including Cribrariales T. Macbr., Liceales E. Jahn, and Trichiales T. Macbr.) and Columellomycetidae Leontyev, Schnittler, S.L. Stephenson, Novozh. & Shchepin (including Clastodermatales Leontyev, Schnittler, S.L. Stephenson, Novozh. & Shchepin, Echinosteliales G.W. Martin, Meridermatales Leontyev, Schnittler, S.L. Stephenson, Novozh. & Shchepin, Stemonitidales T. Macbr., and Physarales T. Macbr.). Within Columellomycetidae, Stemonitidales represents a highly complex and problematic group[1,12–16], especially following recent clarifications regarding the circumscription of Physarales[14,15].

Stemonitidales is notable for its aphanoplasmodia and epihypothallic sporocarp development[13,16]. Members of this order generally share a highly consistent morphology, typically featuring stalked sporocarps, dark spores, and an absence of lime deposits[17,18].

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Despite this apparent morphological uniformity, the circumscription of Stemonitidales has long been debated. Molecular phylogenetic studies now support a core, monophyletic Stemonitidales clade[4], a finding reinforced by subsequent research[19]. It is important to note that this core clade excludes several genera traditionally placed within the order, such as *Lamproderma* Rostaf., *Diachea* Fr., *Diacheopsis* Meyl., *Elaeomyxa* Meyl., *Colloderma* G. Lister[4], and *Meriderma* Mar. Mey. & Poulain[18]. Furthermore, this monophyletic Stemonitidales itself contains numerous unrecognized evolutionary lineages[19–21].

The taxonomic history of Stemonitidales further reflects this complexity. Traditionally, the order contained only one family, Stemonitidaceae Fr., with 15 genera[13]. Subsequent research led to the description of several new genera, such as *Symphytocarpus* Ing & Nann.-Bremek.[22], *Stemonitopsis* (Nann.-Bremek.) Nann.-Bremek.[23], and *Stemonaria* Nann.-Bremek., R. Sharma & Y. Yamam.[24]. Conversely, genera such as *Barbeyella* Meyl., *Clastoderma* A. Blytt, *Diachea*, *Diacheopsis*, *Elaeomyxa*, and *Lamproderma* have been excluded from Stemonitidales[4,15,19,21,25]. Recently, *Valtocarpus* Gmoshinskiy, Prikhodko, Bortnikov, Shchepin & Novozh. was established based on characteristics of *Symphytocarpus* and *Amaurochaete* Rostaf.[19]. These frequent taxonomic changes underscore the limitations of relying on traditional morphological characteristics to define genera within this group. The key characteristics historically used are the presence and completeness of the surface net (an open or closed network at the tips of the capillitial threads on the periphery of the sporotheca) and the presence or absence of a fibrous stalk base[17,18]. These two characteristics have served as the primary characteristics for distinguishing key genera within Stemonitidaceae: *Stemonitis* Gled. (complete surface net and horny stalk), *Stemonaria* (no surface net and fibrous stalk), *Stemonitopsis* (incomplete surface net and horny stalk) and *Symphytocarpus* (incomplete surface net and the formation of pseudoaethalia)[22–24]. This distinction was even elevated to the familial level in the revision by Leontyev et al.[4], who divided the group into Stemonitidaceae (featuring horny stalks) and Amaurochaetaceae Rostaf. ex Cooke (featuring fibrous stalks). However, the completeness of the surface net is often variable[26,27], even within a single specimen. This variability was well established prior to the revision by Leontyev et al.[4], rendering its reliability as a stable taxonomic characteristic questionable. The inconsistency of such core diagnostic characteristics fundamentally explains the instability in the taxonomy of this group.

In contrast, spore ornamentation, a stable and diverse micromorphological characteristic, provides important systematic information, although its taxonomic significance varies across different lineages and taxonomic levels. For instance, spore ornamentation can distinguish *Valtocarpus*[28] from *Symphytocarpus* and *Amaurochaete*. Meanwhile, all species within *Tubifera* J.F. Gmel.[4,29,30], *Siphoptychium* Rostaf.[31], *Thecotubifera* Leontyev, Schnittler, S.L. Stephenson & Novozh.[31], and *Lycogala* Adans.[32–34] possess reticulate spores, making this characteristic alone insufficient to differentiate species within these genera. On the contrary, for *Meriderma*[18,35] and *Trichia* Haller[28], spore ornamentation may be utilized for species differentiation, but not for genus delimitation. Within Stemonitidales, spore ornamentation, which ranges from scattered warts to various types of reticula[36], has also been considered a primary diagnostic characteristic[19]. Based on these observations, this research hypothesizes that, within Stemonitidaceae or the *Stemonitis* s.l. complex, spore ornamentation provides more reliable information regarding phylogenetic relationships compared to the variable and condition-dependent surface net[27] and the structure of the stalk.

To investigate the phylogenetic relationships within Stemonitidales and to identify more taxonomically informative morphological characteristics, this study focuses on Stemonitidaceae with elongated sporocarps, particularly the genera *Stemonitis*, *Stemonaria*, *Stemonitopsis*, and *Symphytocarpus*. Specimens from Belarus, Brazil, China, Japan, Nepal, Russia, the USA, and Vietnam were utilized to construct a detailed phylogeny of Stemonitidales based on three gene markers: nuclear small subunit ribosomal RNA (*nrSSU*), elongation factor-1 alpha (*EF-1α*), and mitochondrial small subunit ribosomal RNA (*mtSSU*). A detailed morphological study was also conducted on selected type specimens of Stemonitidaceae housed in the National Museum of Nature and Science (TNS, Tsukuba, Japan) and in the Fungarium of the Komarov Botanical Institute (LE F, Saint Petersburg, Russia). Comprehensive phylogenetic analyses revealed that Stemonitidaceae is a complex polyphyletic assemblage, although several main clades can be tentatively distinguished. Following the principles of good taxonomic practice developed for myxomycetes[37], and by integrating morphological data from both light and scanning electron microscopy with the phylogenetic results, two new genera are established, 13 new species are described, two previously synonymized species are resurrected, three basionyms are reinstated (replacing currently accepted combinations), and 29 new combinations along with one replacement name are proposed. Species descriptions, illustrations, taxonomic notes, and an updated phylogenetic tree are provided to clarify the placement of the treated taxa.

Materials and methods

Study specimens

In the main analysis, 290 Stemonitidales specimens (including 13 type specimens from herbaria TNS and LE) from Belarus (27), Brazil (two), China (94), Japan (10), Nepal (two), Russia (151, including one from Russian Empire), the USA (one), and Vietnam (three) were selected for morphological and molecular study (Supplementary Table S1). These specimens were deposited in the Herbarium of Fungi of Nanjing Normal University (HFNNU, Nanjing, Jiangsu Province, China), the Herbarium Mycologicum, Academiae Sinicae (HMAS, Beijing, China), the Collection of Myxomycetes at the Department of Mycology and Algology of Lomonosov Moscow State University (MYX, Moscow, Russia; note: collection numbers starting with lowercase 'myx' followed by three digits do not belong to the herbarium MYX but represent nucleotide sequences from GenBank submitted by Thomas Hoppe), LE F (cited simply as LE in this study for convenience), the Herbarium of the Institute of Experimental Botany of the National Academy of Sciences of Belarus (MSK-F, Minsk, Belarus), and TNS.

The nomenclature of myxomycete taxa mentioned in this paper follows the Nomenmyx database[6]. To avoid confusion among genera that share the same initial letter, the following abbreviated prefixes are used in the text: *Comatricha* (*Com.*), *Corallosporopsis* (*Cor.*), *Stemonaria* (*Sta.*), *Stemonitis* (*Ste.*), *Stemonitopsis* (*Stp.*), and *Symphytocarpus* (*Sym.*). For all other genera, the standard single-letter abbreviation (e.g., *A.* for *Amaurochaete*) is employed.

Morphological studies

Photographs of sporocarps from the HMAS, HFNNU, TNS, MSK-F, and a portion of the LE collections were examined and measured in China at Nanjing Normal University using a JSZ6 dissecting microscope (Jiangnan Yongxin Optics Co., Jiangsu Province, China) equipped with an MshOt MSX11 digital camera (Guangzhou

Micro-Shot Technology Co., Ltd, Guangdong Province, China). The remaining LE collections were examined in Russia at the Komarov Botanical Institute RAS using a Zeiss Axio Zoom V16 zoom microscope (Carl Zeiss MicroImaging GmbH, Göttingen, Germany) equipped with an Axiocam 820 color Zeiss digital camera. The MYX collections were examined in Russia at Moscow State University using a Micromed 3 var. 3LED light microscope (Micromed, St. Petersburg, Russia) equipped with an E3CMOS06300 digital camera and epi illumination, or with a Canon 77D digital camera. Image stacks of spores and sporophores taken at different optical sections were processed using focus-stacking software (Helicon Focus v6.0.18).

Microscope slides containing sporocarps from the HMAS, HFNNU, TNS, MSK-F, and a portion of the LE collections were prepared using Hoyer's mounting medium (Phygene Biotech, Fujian Province, China), while those from the MYX and remaining LE collections were mounted in 4% KOH. Observations and measurements of microscopic characteristics were performed with an Olympus BX53 light microscope (Olympus Corporation, Tokyo, Japan) equipped with an MshOt MD50-B digital camera (Guangzhou Micro-Shot Technology Co., Ltd., Guangdong Province, China) and a 0.5× relay lens for the Olympus UIS2 system (Oplenic Optronics, Zhejiang Province, China), an Axio Imager A1 light microscope (Carl Zeiss MicroImaging GmbH, Göttingen, Germany) equipped with an Axiocam 807 color Zeiss digital camera, and a Micromed 3 var. 3LED light microscope equipped with an E3CMOS06300 digital camera. The diameters of more than 50 spores from each specimen were measured, including ornamentation, using an oil immersion objective at a magnification of 100×[38]. The diameters of more than 50 surface net meshes from each specimen were measured using an oil immersion objective at a magnification of 40×. The range of variation in diameter is presented in descriptions as rounded values in the format: (minimum–)25th percentile–75th percentile(–maximum)[39].

For scanning electron microscopy (SEM) observations, air-dried specimens were mounted on aluminum stubs using adhesive tape, sputter-coated with gold or a gold-palladium alloy, and observed at 15 kV under a Phenom XL G2 scanning electron microscope (Phenom Scientific, Eindhoven, Netherlands) at Nanjing Normal University, China[34]. In Russia, similarly prepared specimens were examined at 15 kV using a Quattro S scanning electron microscope (Thermo Fisher Scientific, Waltham, MA, USA) at Moscow State University and a Jeol JSM-6390 LA scanning electron microscope (JEOL Ltd, Tokyo, Japan) at the Komarov Botanical Institute[19].

To illustrate differences in the color of the spore mass, sporocarps of different species were affixed side by side on transparent double-sided tape in three sets, imaged on a Zeiss Axio Zoom V16 zoom microscope at the same magnification and with identical lighting settings, and subsequently combined into a single collage in a graphics editor without further processing.

The terminology used to describe spore ornamentation patterns followed the definitions provided by Rammeloo[36].

DNA extraction, PCR amplification, and sequencing

Approximately 10 mg of sporocarp tissue from each specimen was picked up with forceps under a dissecting microscope (DM) and placed in a sterile 1.5 mL Eppendorf tube containing three glass beads with a diameter of 2.5 mm. DNA extraction followed the protocol of the DP316 TIANamp Micro DNA Kit (Tiangen Biotech, Beijing, China).

To reconstruct the phylogeny of Stemonitidales, three independent genetic markers (*nrSSU*, *EF-1α*, and *mtSSU*) were targeted for sequencing. Approximately 550–750 base pairs (bp) from the 5′ end of *nrSSU*, a fragment free of introns, were amplified with forward primers S1 or S2[40] and reverse primers SU19R[41] or SSU_rev[15]. Overlapping fragments of the protein-coding gene for *EF-1α* were amplified with primer pairs PB1F/PB1R (approximately 800 bp)[42], a set of primers for a semi-nested polymerase chain reaction (PCR) EF03 (EF04*)/KEF_R3 (approximately 1,000 bp)[43,44], and STE_EF_F1/STE_EF_R1 (designed for this study, approximately 500 bp). The asterisk (*) designates that the primer was used in a semi-nested PCR. In addition, partial sequences of *mtSSU* (approximately 400 bp) were obtained with a set of primers Kmit_F (Kmit_Fi*)/Kmit_R[45] for a semi-nested PCR.

A list of primers, their sequences, and PCR amplification protocols for different primer combinations is provided in Table 1. The composition of PCR reactions has been described previously by Song et al.[34]. All PCR products were sequenced using the Sanger method by Jiangsu CoWin Biotech Co., Ltd. (Taizhou, Jiangsu Province, China).

Sequence alignment and phylogenetic analyses

A comprehensive search of the NCBI GenBank database was conducted to retrieve *nrSSU*, *EF-1α*, and *mtSSU* sequences associated with species of Stemonitidales and Physarales. The final dataset consisted of a total of 735 sequences, including 479 (217 *nrSSU*, 148 *EF-1α*, and 114 *mtSSU*) newly obtained sequences from 232

Table 1. Primer pairs and amplification protocols used in this study.

Gene	Name	F/R	Sequence (5′–3′)	Amplification protocol
nrSSU	S1	F	AACCTGGTTGATCCTGCC	2 min at 98 °C, 35 cycles (10 s at 95 °C, 10 s at 56 °C, 15 s at 72 °C) and 5 min at 72 °C
	S2	F	TGGTTGATCCTGCCAGTAGTGT	
	SU19R	R	GACTTGTCCTCTAATTGTTACTCG	
	SSU_rev	R	AGACTTGTCCTCYAATTGTTAC	
EF-1α	PB1F	F	ACCCGTGAGCACGCTCTCCT	2 min at 98 °C, 35 cycles (10 s at 98 °C, 10 s at 65.4 °C, 10 s at 72 °C) and 5 min at 72 °C
	PB1R	R	CGCACATGGGCTTGGAGGGG	
	EF03	F	TGATCTACAAGTGCGGTG	2 min at 98 °C, 35 cycles (10 s at 98 °C, 10 s at 60 °C, 15 s at 72 °C) and 5 min at 72 °C
	EF04*	F	TGGGTGTTGGACAAACTC	
	KEF_R3	R	CCGTTCTTGATGTTCTTGG	
	STE_EF_F1	F	TTCGAGGCTGGTATTGCCAAG	2 min at 98 °C, 35 cycles (10 s at 98 °C, 10 s at 60.4 °C, 15 s at 72 °C) and 5 min at 72 °C
	STE_EF_R1	R	ACGTTGAACCCGACGTTGT	
mtSSU	Kmit_F	F	AGTGTTATTCGTGATGACTGG	2 min at 98 °C, 35 cycles (10 s at 95 °C, 10 s at 56 °C, 15 s at 72 °C) and 5 min at 72 °C
	Kmit_Fi*	F	ATGACTGGGCGTAGGGTA	
	Kmit_R	R	CGAATTAAACCACATCTCCACC	

Note: *nrSSU*, nuclear small subunit ribosomal RNA; *EF-1α*, elongation factor-1 alpha; *mtSSU*, mitochondrial small subunit ribosomal RNA. The asterisk (*) designates that the primer was used in a semi-nested polymerase chain reaction.

specimens (Supplementary Table S1) and 256 sequences (128 *nrSSU*, 71 *EF-1α*, and 57 *mtSSU*; Supplementary Table S2) retrieved from GenBank (Supplementary Files S1–S3).

The *nrSSU*, *EF-1α*, and *mtSSU* sequences were aligned using MAFFT v7.471[46] with the E-INS-i option for *nrSSU* and *mtSSU*, and the G-INS-i option for *EF-1α*, applying default gap penalties[47] in PhyloSuite v1.2.3[48,49]. For the protein-coding *EF-1α* sequence, intronic regions were identified and manually removed by comparison with the annotated *Badhamia polycephala* (Schwein.) J.M. García-Martín, J.C. Zamora & Lado (≡ *Physarum polycephalum* Schwein.) sequence (GenBank accession number: AF016243). Subsequently, ambiguously aligned fragments, primer binding sites, gaps, and low-quality ends were removed using Gblocks[50] with the following parameter settings: minimum number of sequences for a conserved/flank position = 173/173 for *nrSSU*, 110/110 for *EF-1α*, and 86/86 for *mtSSU*; maximum number of contiguous non-conserved positions = 12, minimum length of a block = 10, allowed gap positions = all). This filtering process was particularly crucial for mitigating alignment uncertainties in the *mtSSU* dataset caused by inherent mRNA editing and varying sequence lengths (including longer sequences retrieved from GenBank).

A three-gene phylogeny was built from a concatenated dataset of Gblocks-filtered sequences with the following partition: *nrSSU* 1–540, *EF-1α* 541–1,497, and *mtSSU* 1,498–1,970 (Supplementary Files S4–S6). The best-fit model of nucleotide substitution was determined by ModelFinder[51] for each partition using the corrected Akaike Information Criterion (AICc): JC + G4 for *nrSSU*, JC + G4 for the first codon position of *EF-1α*, JC for the second codon position, JC for the third codon position, and TPM2 + F + I + G4 for *mtSSU*. Maximum likelihood (ML) analyses were conducted with IQ-TREE v1.6.8[52,53]. The ultrafast bootstraps (UBS) analysis with 1,000 pseudoreplicates was performed to evaluate the statistical support of clades. Additionally, the transfer of bootstrap expectation (TBE)[54] was calculated using the online platform BOOSTER (https://booster.pasteur.fr) with 1,000 standard bootstrap replicates to account for the effect of rogue taxa in branch supports.

The best fitting substitution models for Bayesian inference (BI) analysis were as follows: JC + G4 for *nrSSU*, JC for the first codon position of *EF-1α*, JC + G4 for the second codon position, JC for the third codon position, and GTR + F + I + G4 for *mtSSU*. BI analyses were conducted using MrBayes v3.2.6[55], with four separate chains, each 10 million generations long (sampling every 1,000th generation). The convergence of Markov Chain Monte Carlo (MCMC) simulations was estimated using Tracer 1.7.2[56] and by the average standard deviation of split frequencies. Consequently, the first 19% of sampled data and trees were discarded as burn-in.

ML and BI trees were visualized in iTOL[57]. *Echinostelium bisporum* (L.S. Olive & Stoian.) K.D. Whitney & L.S. Olive (herbarium number: Nx14-A1), *Echinosteliopsis oligospora* D.J. Reinh. & L.S. Olive (herbarium number: HH14-A2-1A), and *Barbeyella minutissima* Meyl. (herbarium number: LE317265) were used to root the trees[19]. The ML tree topology was used as the base, and both the Bayesian posterior probabilities (PP) and TBE values were mapped onto the corresponding nodes using Adobe Illustrator 2026 (San Jose, CA, USA).

To verify the exclusivity of genotypes for the delineated species and assess single-gene topological discordance, individual phylogenetic trees were additionally reconstructed for each of the three markers (*nrSSU*, *EF-1α*, and *mtSSU*). The sequence alignments and ML analyses for these single-gene datasets followed the identical protocols and parameters described above for the concatenated dataset, with branch supports evaluated via 1,000 ultrafast bootstrap replicates.

Taxonomic framework and delimitation criteria

To ensure methodological consistency and address the common challenge of missing molecular data for historical species, a hierarchical framework was established for delimiting genera and assigning species. This framework combines phylogenetic and morphological evidence, enabling the categorization of all treated taxa.

Generic delimitation: The recognition of a genus is based on two principal criteria: 1) the monophyly of the group, and 2) the presence of one or more key diagnostic morphological characteristics that are both shared by the vast majority of members of the genus (a secondary loss is possible) and unique or nearly unique to it within related taxa. In this study, these characteristics predominantly manifest as sporotheca color and distinct spore ornamentation patterns under SEM. Except for *Stemonaria* (must be disbanded, see Notes of the genus) and *Symphytocarpus*, all other genera treated or established simultaneously satisfy both criteria. However, for *Symphytocarpus*, the phylogenetic positions of critical species are unstable, challenging the criterion of strict monophyly. In this specific instance, to avoid premature and potentially destabilizing taxonomic changes, a stronger reliance is temporarily placed on a consistent morphological diagnosis (criterion 2) to maintain a coherent generic concept, with the expectation that future phylogenetic studies will clarify these relationships.

Consequently, species are categorized as: A) Accepted species for which molecular data, either generated in this study or previously published, are available, and which correspond to previously studied type specimens or align convincingly with the generally accepted species concept (including morphological, geographical, ecological, and other criteria); B) Morphospecies included in the genus but not yet phylogenetically studied that are formally transferred (a new combination is proposed) based on direct study of the type material, authenticated material, or specimens from the type region, confirming they possess the diagnostic morphological characteristics of the genus. A reliable and detailed protologue may suffice for this assessment if physical material is unavailable; C) Temporarily and formally recognized species (applicable within *Stemonaria*, *Stemonitis*, *Stemonitopsis*, and *Symphytocarpus*) that currently lack detailed morphological data from type or other material and phylogenetic data, or for which the study of available material yields insufficient evidence to support a revision of their generic placement. The fact that these species exist is not in doubt, but these species retain their existing generic name until more conclusive data (e.g., molecular sequences or higher-quality morphological studies) become available.

Results

Phylogeny

A total of 479 nucleotide sequences were generated in this study, comprising 217 *nrSSU*, 148 *EF-1α*, and 114 *mtSSU* sequences from 232 specimens (Supplementary Table S1). The final phylogenetic analysis was based on 735 sequences obtained from 355 specimens, comprising 345 *nrSSU*, 219 *EF-1α*, and 171 *mtSSU* sequences (Supplementary Tables S1, S2).

The topologies of ML and BI trees were similar. The ML tree is shown in Fig. 1. A clade containing *Argentoderma typhinum* (UBS/PP/TBE = 100/100/100) forms the basal lineage relative to Meridermatales, Physarales, and Stemonitidales. The Meridermatales, represented by members of *Meriderma*, are recovered as a fully supported clade (UBS/PP/TBE = 100/100/100). The Physarales

clade (UBS/PP/TBE = 98/95/84) contains a mixed assemblage of *Lamproderma* and *Diacheopsis* (UBS/PP/TBE = 100/-/100), species alongside typical Physaraceae genera, including *Badhamia* Berk. (UBS/PP/TBE = 85/-/96), *Craterium* Trentep. (UBS/PP/TBE = 100/100/100), *Diachea* (UBS/PP/TBE = 100/100/100), *Diderma* Pers. (UBS/PP/TBE = 100/100/100), *Didymium* Schrad. (UBS/PP/TBE = 100/100/100), *Fuligo* Haller (UBS/PP/TBE = 100/100/100), *Nannengaella* J.M. García-Martín, J.C. Zamora & Lado (UBS/PP/TBE = 100/-/79), *Physarum* Pers. (UBS/PP/TBE = 100/100/100), and *Polyschismium* Corda (UBS/PP/TBE = 100/100/100).

Between Meridermatales and Stemonitidales, *Lamproderma cacographicum*, *Lamproderma sauteri*, and *Comatricha irregularis* form a monophyletic group that receives only partial support (UBS/PP/TBE = 86/-/-).

Members of Stemonitidales constitute a strongly supported monophyletic lineage (UBS/PP/TBE = 97/-/-); however, relationships within the order are complex. Taxa traditionally assigned to Amaurochaetaceae[4] do not form a monophyletic group but appear paraphyletic. Species of *Amaurochaete* (*A. atra*, *A. comata*, *A. macrospora,* and *A. tubulina*) cluster together with full support (UBS/PP/TBE = 100/100/100), whereas members of *Paradiacheopsis* Hertel, *Comatricha* Preuss, and *Enerthenema* Bowman form some weakly supported clades.

The family Stemonitidaceae exhibits even more intricate phylogenetic relationships than previously recognized. Although its members collectively form a highly supported monophyletic group (UBS/PP/TBE = 97/99/-), several stable subclades can be distinguished: (1) a moderately supported monophyletic *Corallosporopsis*

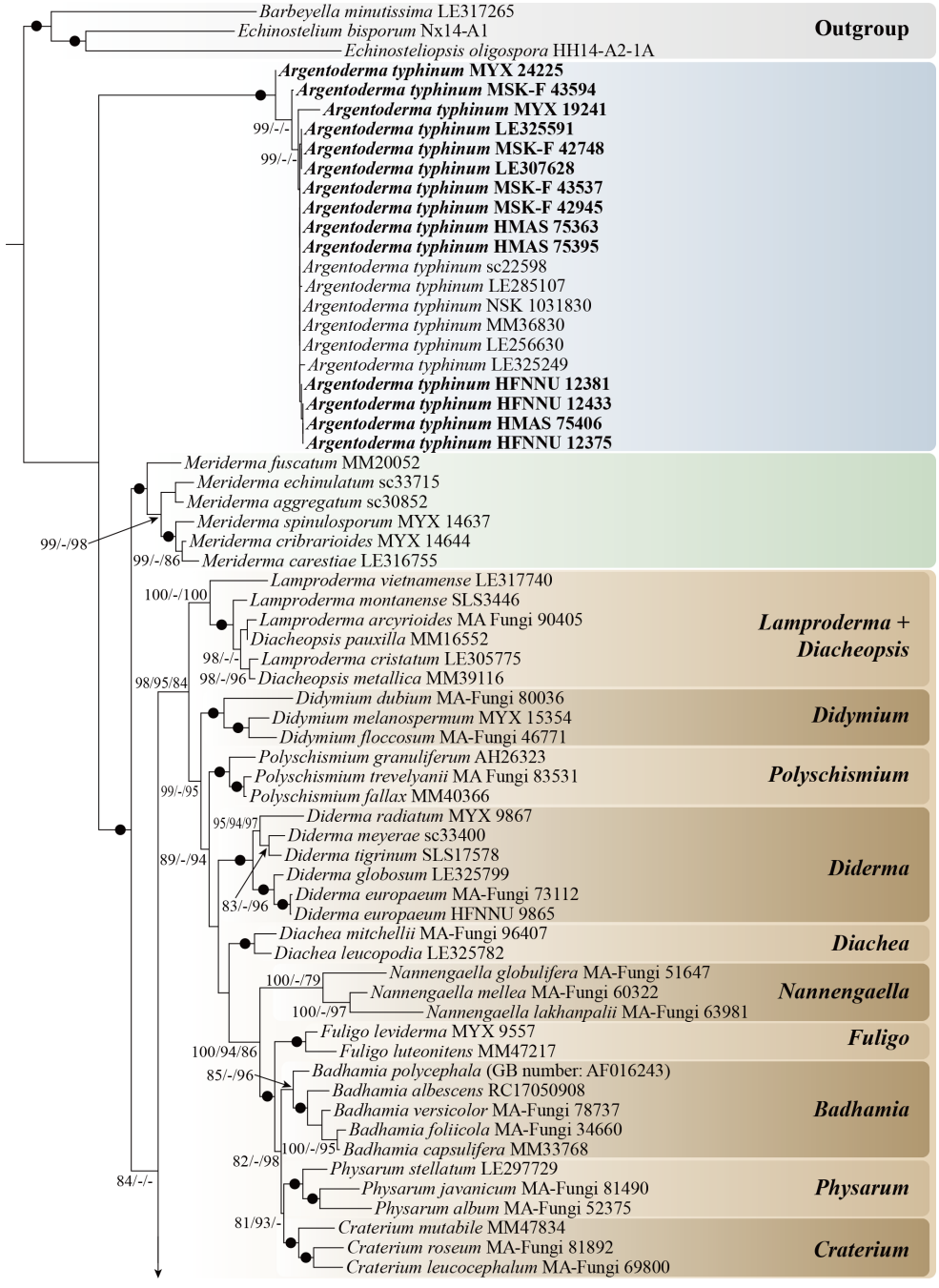

Fig. 1 to be continued

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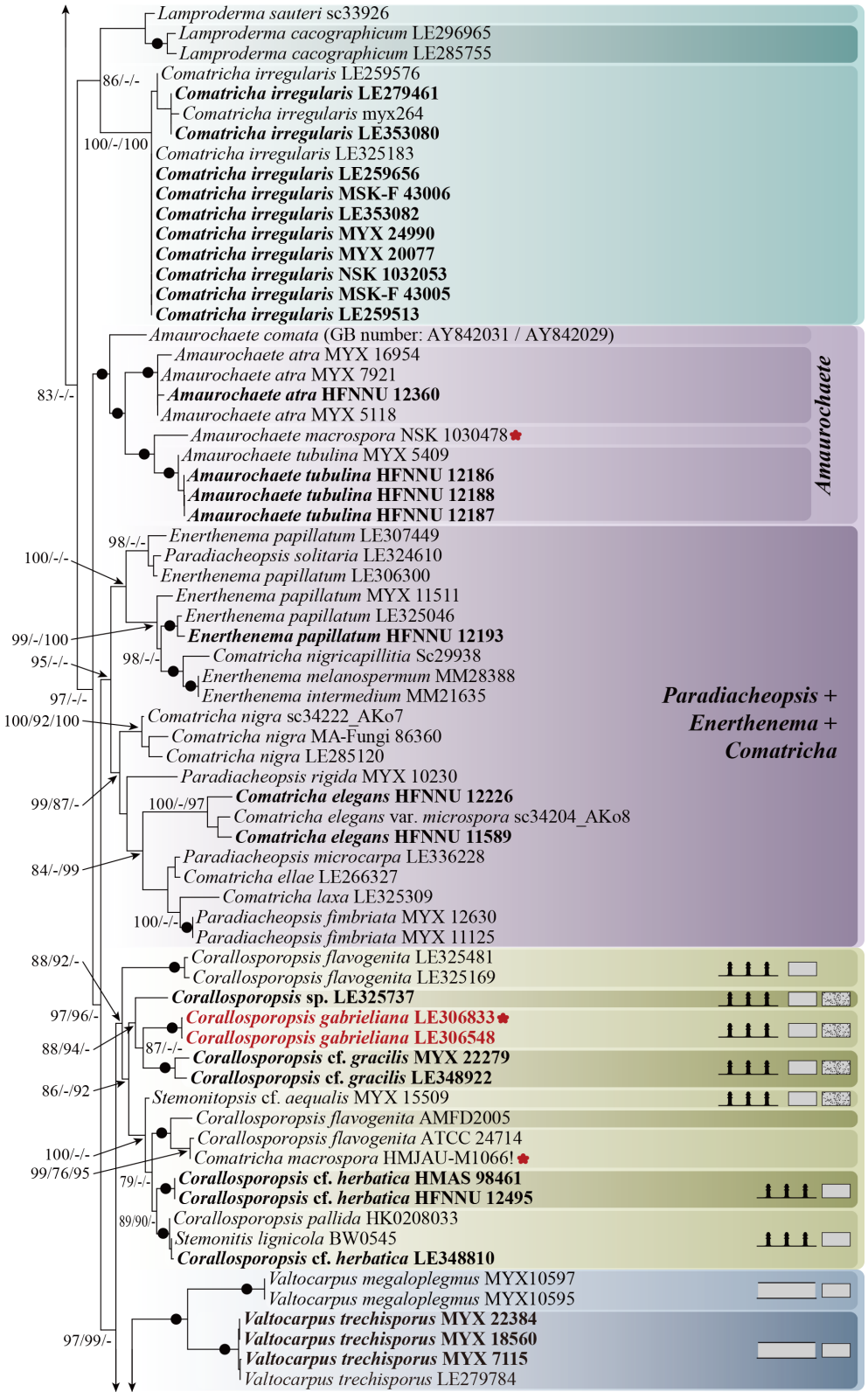

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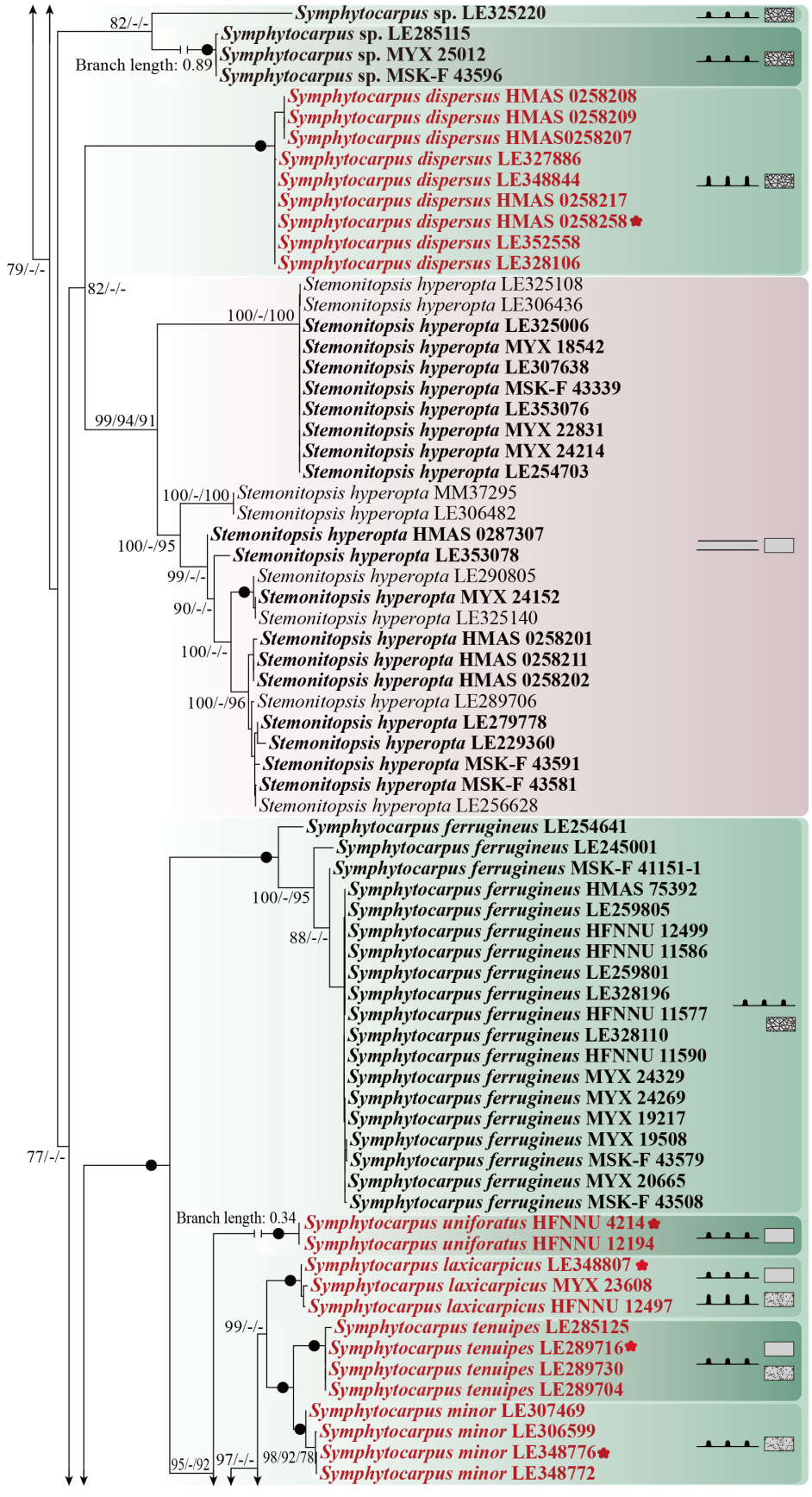

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Fig. 1 to be continued

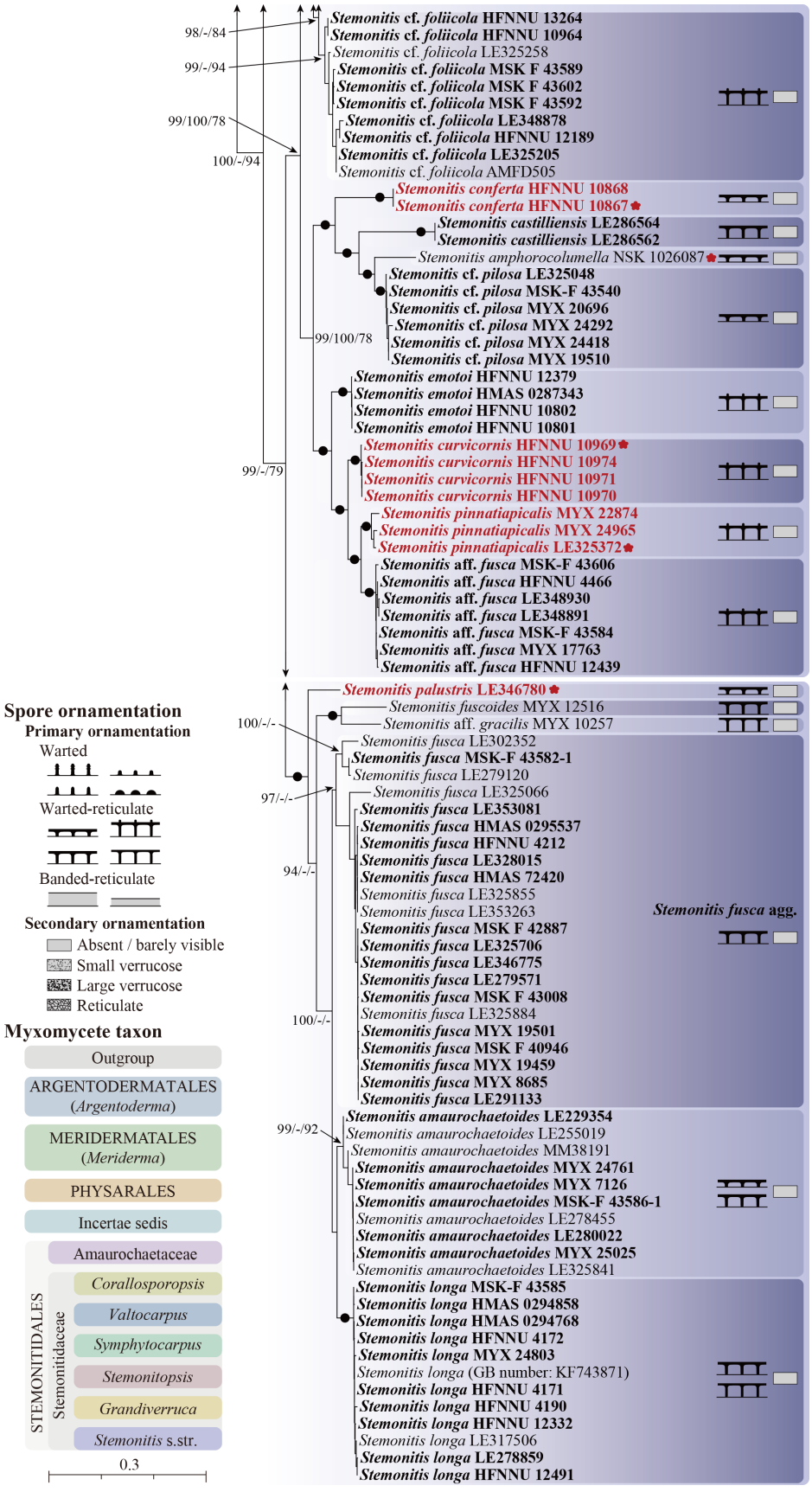

Fig. 1 Maximum likelihood tree from the concatenated *nrSSU*, *EF-1α*, and *mtSSU* sequences, showing phylogeny of Stemonitidales. Only nodes with UBS/PP/TBE ≥ 70/70/70 are shown. The voucher numbers are indicated after the species names. Newly obtained sequences in this study are indicated in bold, new species described in this study are indicated in red, and holotype or isotype specimens are marked with red stars. The scale bar represents the number of substitutions per site.

clade (UBS/PP/TBE = 88/92/-) containing *Cor. flavogenita*, *Cor. gabrieliana*, *Cor.* cf. *gracilis*, *Cor. herbatica*, *Cor. pallida*, *Stemonitopsis* cf. *aequalis* MYX 15509, and *Comatricha macrospora* HMJAU-M1066; (2) a robust *Valtocarpus* clade (UBS/PP/TBE = 100/100/100) composed of *V. megaloplegmus* and *V. trechisporus*; (3) a moderately supported *Stemonitopsis* clade (UBS/PP/TBE = 99/94/91) containing *Stemonitopsis hyperopta* agg.; (4) a strongly supported *Symphytocarpus* clade (UBS/PP/TBE = 100/100/100) comprising *Sym. ferrugineus*, *Sym. uniforatus, Sym. laxicarpicus, Sym. tenuipes, Sym. minor, Sym. flaccidus*, *Sym. pseudoflavogenitus*, and *Sym. splendens*; (5) a strongly supported *Grandiverruca* clade (UBS/PP/TBE = 100/100/100) consisting of *G.* cf. *smithii* and *G. verrucosifila*; and (6) a monophyletic *Stemonitis* s.str. clade (UBS/PP/TBE = 100/-/94), containing *Ste. amaurochaetoides*, *Ste. amphorocolumella*, *Ste. castillensis*, *Ste. conferta*, *Ste. curvicornis*, *Ste. emotoi*, *Ste*. cf. *foliicola*, *Ste. fusca*, *Ste. fuscoides*, *Ste. gracilis*, *Ste. imperfecta*, *Ste. longa*, *Ste. palustris*, *Ste.* cf. *pilosa*, *Ste.* cf. *pinicola*, *Ste. pinnatiapicalis*, and *Ste. spinimuralis*.

The phylogenetic positions of several other specimens remain less resolved: *Symphytocarpus* sp. LE325220 and *Symphytocarpus* sp. (LE285115, MSK-F 43596, MYX 25012) form a moderately supported monophyletic group (UBS/PP/TBE = 82/-/-), while *Symphytocarpus dispersus* is nested within the *Stemonitopsis* clade (UBS/PP/TBE = 82/-/-), indicating that its generic placement requires further study.

Furthermore, individual ML phylogenies inferred from the *nrSSU*, *EF-1α*, and *mtSSU* alignments (Supplementary Figs S1–S3) revealed that each recognized taxon possesses unique genetic variants across all studied markers, with no identical sequences shared between different species.

Taxonomy

• *Amaurochaete* Rostaf., Versuch eines Systems der Mycetozoen: 8 (1873)

MycoBank number: MB12007.

Type: *Amaurochaete atra* (Alb. & Schwein.) Rostaf., Versuch eines Systems der Mycetozoen: 8 (1874).

Accepted species: *Amaurochaete atra* (Alb. & Schwein.) Rostaf., *A. comata* G. Lister & Brândza, *A. macrospora* (A. Vlasenko) W.L. Song, A. Vlasenko, Bortnikov & Gmoshinskiy, and *A. tubulina* (Alb. & Schwein.) T. Macbr.

Morphospecies included in the genus but not yet phylogenetically studied: *Amaurochaete fusiformis* (Nann.-Bremek. & Härk.) H. Marx & A. Kuhnt.

Notes: Molecular data are currently available for nearly all recognized species of *Amaurochaete*, including *A. atra*, *A. comata*, *A. tubulina*, and *A. macrospora*. These species share similar morphological characteristics, including aethalia or pseudoaethalia, a black spore mass, and large spores (exceeding 12 μm in diameter) with an unevenly thickened wall bearing a light spot. Under SEM, the spore ornamentation conforms to the pilate type, with relatively small pili that are slightly widened at the apex (*A. macrospora* in Vlasenko et al.[58]; *A. atra* MYX 16954 in Gmoshinskiy et al.[19]: fig. 4h; *A. tubulina* MYX 5409 in Gmoshinskiy et al.[19]: fig. 4p; *A. comata* in Moreno et al.[59]: fig.1e–g).

The only species lacking genetic data is *A. fusiformis*. This rare species was originally described as *Symphytocarpus fusiformis* Nann.-Bremek. & Härk. due to its evanescent peridium[60], but was recently transferred to *Amaurochaete* based on the study of a specimen from Germany[61]. This species differs from other *Amaurochaete* species in its smaller and lighter spores. Given the absence of molecular data and these notable morphological differences, its placement remains doubtful. It is temporarily retained in *Amaurochaete* pending the acquisition of molecular data.

***Amaurochaete macrospora* (A. Vlasenko) W.L. Song, A. Vlasenko, Bortnikov & Gmoshinskiy, comb. nov.**

MycoBank number: MB838364.

Basionym: *Symphytocarpus macrosporus* A. Vlasenko, Karstenia 58 (2): 395 (2020).

Notes: *Symphytocarpus macrosporus* was first described from Russia[58]. Morphologically, *Sym. macrosporus* is similar to *A. comata*, as both species occur on the bark of coniferous trees and feature large, dark, warted spores. Vlasenko et al.[58] placed *Sym. macrosporus* in *Symphytocarpus* primarily based on its thin, membranous, mostly fugacious peridium. However, Vlasenko et al.[58] also noted that the peridium of this species is mostly evanescent at an early stage. Furthermore, considering the typical characteristics of its sporocarps, which are curved and densely packed into a cushion-like pseudoaethalium, *Sym. macrosporus* better fits the definition of *Amaurochaete*[17,22]. In the three-gene phylogenetic tree constructed in this study, the holotype of *Sym. macrosporus* (NSK 1030478) forms a well-supported sister group with *A. tubulina* (UBS/PP/TBE = 100/100/100; Fig. 1) and is consistently placed within the *Amaurochaete* clade. Therefore, based on the combination of its morphological characteristics and molecular phylogenetic evidence, *Sym. macrosporus* is herein transferred to *Amaurochaete* as *A. macrospora*.

• *Corallosporopsis* W.L. Song, Bortnikov, Gmoshinskiy, Shuang L. Chen & Novozh., gen. nov.

MycoBank number: MB863053.

Etymology: from the Latin *corallium* and *spora*, referring to the apically thickened bacula of the spore ornamentation, which is a diagnostic characteristic for the genus. (non *Corallospora* Werderm., an ascomycete from Sordariomycetes).

Type (designated here): *Corallosporopsis gabrieliana* Bortnikov, W.L. Song, Shuang L. Chen & Novozh.

Diagnosis: Sporocarps relatively small, ovoid to elongated and cylindrical, stalked. Peridium fugacious. Spores pale brown, brown, or orange-brown in mass, ornamented with bacula with expanded to coralloid tips, which can be seen under SEM (warted to spinulose in LM).

Description: Sporocarps solitary to densely gregarious, mostly (1–)3–6(–8) mm in total height. Stalk conspicuous, not exceeding 1/3 of the total height. Columella tapering upwards, filamentous, often expanded at the apex. Capillitium dense, often sinuous, branching points sometimes with irregular membranous expansions, threads bearing conspicuous, irregular small warts under SEM. Surface net absent, incomplete or complete, with distinct meshes, sometimes with small pointed free ends, threads bearing conspicuous, irregular small warts under SEM. Spores pale brown, brown, or orange-brown in mass, ornamented with irregularly distributed bacula with expanded to coralloid tips.

Accepted species: *Corallosporopsis flavogenita* (E. Jahn) Bortnikov, W.L. Song & Novozh., *Cor. gabrieliana* Bortnikov, W.L. Song, Shuang L. Chen & Novozh., *Cor. gracilis* (G. Lister) Bortnikov, W.L. Song & Novozh., *Cor. herbatica* (Peck) W.L. Song, Bortnikov, Shuang L. Chen & Novozh., and *Cor. spinispora* (Novozh. & D.W. Mitch.) Bortnikov, Gmoshinskiy, W.L. Song & Novozh.

Morphospecies included in the genus but not yet phylogenetically studied: *Corallosporopsis capillitionodosa* (G. Moreno, D.W. Mitchell, C. Rojas & S.L. Stephenson) Bortnikov, W.L. Song & Novozh., *Cor. laxifila* (Nann.-Bremek. & Y. Yamam.) W.L. Song, Bortnikov, Shuang L. Chen & Novozh., *Cor. mediterraneensis* (H.H. Doğan & Eroğlu) Gmoshinskiy, W.L. Song & Bortnikov, *Cor. pallida* (Wingate) Bortnikov, W.L. Song & Novozh., *Cor. pulchella* (C. Bab.) Bortnikov,

W.L. Song & Novozh., and *Cor. pallidofila* (Y. Yamam. & Nann.-Bremek.) W.L. Song, Bortnikov, Shuang L. Chen & Novozh.

Notes: The primary diagnostic characteristic of *Corallosporopsis* is its spore ornamentation, which consists of large, irregularly distributed bacula with characteristically expanded coralloid tips. This trait, best observed under SEM at high magnifications, is not found in other phylogenetic lineages and is considered unique to the genus. All molecularly studied specimens possess relatively small, elongate-cylindrical sporocarps measuring (1–)3–6(–8) mm in total height. For many such species, high-quality SEM photographs of type specimens clearly show the apically expanded bacula, confirming their placement in *Corallosporopsis*.

Nevertheless, the application of this diagnostic trait requires careful evaluation, as illustrated by the complex case of *Comatricha macrospora* B. Zhang & Yu Li. This species was described from China[62] and is characterized by a persistent peridium, large spores (11–14 μm in diameter), and a densely, evenly, and minutely warted ornamentation. While SEM images of the holotype spores (see Zhang et al.[62]: fig. 2f) suggest the warts possess apical thickenings, and a published *nrSSU* sequence from the holotype (GenBank number: MG867573) groups within the *Corallosporopsis* clade, where it forms a well-supported group (UBS/PP/TBE = 99/76/95; Fig. 1) with *Cor. flavogenita* ATCC 24714 and *Cor. flavogenita* AMFD2005, the combination of its persistent peridium (atypical for the genus) and the potential for DNA sample contamination raises significant doubt about its placement. Consequently, the evidence for its transfer to *Corallosporopsis* is considered inconclusive, and this study refrains from proposing a new combination at this time, pending a definitive re-examination of the type material.

Several species historically classified in *Comatricha* and *Macbrideola* H.C. Gilbert, often with very small, globose to subglobose sporothecae, possess spores with enlarged bacula visible in published SEM photographs, suggesting a potential affinity with *Corallosporopsis*. A representative and taxonomically debated example is *Comatricha brachypus* (Meyl.) Meyl. Although currently treated as a synonym of *Comatricha pulchella* (C. Bab.) Rostaf.[6], it is considered distinct by some authors based on its larger spores (9–11 μm vs 6.5–8.5 μm)[18,63,64]. A specimen identified as *Com. brachypus* (MYX 25105; spores 10.1–10.6 μm in diameter) was examined (Supplementary Fig. S4), and SEM analysis confirmed that its bacula have the expanded apices (Supplementary Fig. S4c, S4d) characteristic of *Corallosporopsis*.

Other species with similar spore morphology include *Comatricha canariensis* G. Moreno, A. Sánchez & López-Vill. (see Moreno et al.[65]: fig. 3g–i), *Comatricha pellucida* G. Moreno & Illana (see Moreno et al.[66]: figs 23–26), *Macbrideola ovoidea* Nann.-Bremek. & Y. Yamam. (see Moreno et al.[67]: fig. 2f, g), and *Macbrideola rutilipedata* (H. Marx) G. Moreno, Seraoui, Mar. Mey. & López-Vill. (see Moreno et al.[67]: fig. 3j–m). Although spore ornamentation aligns these taxa with *Corallosporopsis*, and sporocarp size alone is not a reliable generic criterion, they lack supporting molecular data. Furthermore, the current morphological concept of *Corallosporopsis* is primarily based on species with larger, elongate-cylindrical sporocarps. Whether these small, globose-sporotheca taxa represent the same evolutionary lineage requires phylogenetic testing. Therefore, following the established taxonomic framework (Criterion C), this study refrains from proposing new combinations for them within *Corallosporopsis* pending phylogenetic confirmation from type or topotypic material. This conservative approach acknowledges the suggestive morphology while highlighting the need for further evidence.

***Corallosporopsis capillitionodosa* (G. Moreno, D.W. Mitchell, C. Rojas & S.L. Stephenson) Bortnikov, W.L. Song, Gmoshinskiy & Novozh., comb. nov.**

MycoBank number: MB863314.

Basionym: *Stemonitis capillitionodosa* G. Moreno, D.W. Mitchell, C. Rojas & S.L. Stephenson, Bol. Soc. Micol. Madrid 34: 200 (2010).

Notes: *Stemonitis capillitionodosa* is a species described based on the study of a 1922 specimen from Costa Rica[68]. It is characterized by small sporocarps (3–6 mm in total height), a large-meshed capillitium with expansions at the axils, an expanded columella apex, and spores ornamented with apically expanded warts (bacula), as clearly demonstrated in the published SEM micrographs of the type material (see Moreno et al.[68]: figs 15–17). All three characteristics correspond well with the diagnosis of *Corallosporopsis*, and the transfer to *Corallosporopsis* is considered justified, although molecular data and more recent findings of this species are not yet available.

It should be noted that two specimens collected in Russia were previously misidentified as *Ste. capillitionodosa*[69,70]. However, additional detailed study of the morphology of these specimens justified their description as a species new to science, *Cor. gabrieliana*, which was also selected as the type for the new genus *Corallosporopsis* (see below).

***Corallosporopsis flavogenita* (E. Jahn) Bortnikov, W.L. Song & Novozh., comb. nov.**

MycoBank number: MB863315.

Basionym: *Stemonitis flavogenita* E. Jahn, Verh. Bot. Ver. Prov. Brandenb.: 165 (1904).

Materials examined: RUSSIA, Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.9238° N, 158.7063° E, on decayed log, 14 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325169); Kamchatka Territory, Milkovsky District, vicinity of Lazo village, 55.4493° N, 159.7981° E, on mosses, 19 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325481).

Notes: *Stemonitis flavogenita* usually forms sporocarps on rotten wood. This species is characterized by elongate sporocarps (4–8 mm in total height) on short stalks (up to 1/3 of the total height), capillitium with membranous expansions and a delicate, well-formed surface net bearing many small pointed free ends, a columella that terminates in a funnel-shaped membranous expansion at the apex, and spores measuring 7–9.6 μm in diameter[71]. Based on these morphological characteristics, particularly the presence of bacula with apically thickened tips in the specimens examined in this study, align with the diagnosis of *Corallosporopsis*. Consequently, the species is transferred to *Corallosporopsis* as *Cor. flavogenita*. Phylogenetically, specimens currently identified as *Cor. flavogenita* form at least two independent, well-supported clades (Fig. 1), a result consistent with observed morphological variation and underscoring the need for further study of material historically assigned to this name.

It has previously been shown that in closely related species, *Cor. pallida* (≡ *Stemonitis pallida* Wingate) and *Cor. herbatica* (≡ *Stemonitis herbatica* Peck), morphogenesis may not proceed properly, and the columella may have extensions[72–75]. *Corallosporopsis pallida* differs in its smaller spores ([6.0–]6.5–7.5[–8.0] μm in diameter) and, according to Moreno et al.[71], the main differences between *Cor. flavogenita* and *Cor. pallida* are: '… the combination of the characteristics of rather thick branches in the surface net and a darker brown color of the inner capillitium'. *Corallosporopsis herbatica*, which typically occurs on living plants or leaf litter (rarely on dead wood)[13], bears short-stalked sporocarps[71] and has a nearly complete surface net that usually lacks numerous pointed free ends, although its spore size (7.3–9 μm in diameter) is similar[74,76]. The two species can be further separated by the lighter,

warty spores with a distinct germination pore and the spiked surface net in *Cor. flavogenita*[74,76].

***Corallosporopsis gabrieliana* Bortnikov, W.L. Song, Shuang L. Chen & Novozh., sp. nov. Fig. 2**

MycoBank number: MB863073.

Etymology: The species is named in honor of Dr. Gabriel Moreno in appreciation of his many years of contribution to the study of numerous Stemonitidales species, including the study of many type specimens, which were of considerable assistance in preparing this study[68,71,77,78].

Holotype: RUSSIA, Murmansk Region, Monchegorsk Municipal District, Laplandskiy State Nature Biosphere Reserve, 67.6838° N, 32.3646° E, on decayed wood of *Pinus sylvestris*, 26 Aug 2015, field, leg. Novozhilov Yu.K., Shchepin O.N., Erastova D.A., and Tikhonova E.N. (LE306833, GenBank *nrSSU*: MN610391; *EF-1α*: PZ188771; *mtSSU*: PZ160575).

Diagnosis: Sporocarps clustered, 3–6 mm in total height; sporotheca cylindrical, nut brown to reddish brown, with rounded or blunt apex; stalk 15%–25% of the total height; columella with funnel-shaped expansion; surface net well-developed to somewhat irregular. meshes 10–30(–80) μm in diameter; spores (8.4–)9.2–10.2(–10.6) μm in diameter, with expanded bacula.

Description: Sporocarps clustered, cylindrical, 3.0–5.6 mm in total height. Sporotheca cylindrical, slightly rounded or blunt at the top, 0.3–0.6 mm thick, brown with a reddish tint. Stalk relatively short, 15%–26% of the total height of the sporocarps, 31–86 μm thick, often slightly flattened, as if collapsed inward. Hypothallus common to the group of sporocarps, hyaline to reddish brown, shiny. Peridium evanescent. Columella cylindrical, ending just below the sporotheca apex with a funnel-shaped expansion. Capillitium dense, pale brown to brown, extending along the entire length of the columella, forming an internal net with sometimes sparse, sometimes abundant membranous expansions. Surface net well-developed, somewhat irregular; meshes vary greatly in size, (5–)8–31(–76) μm in diameter, with free ends. Spore concolorous with the sporotheca in mass, pale brown in transmitted light, globose to subglobose, (8.4–)9.2–10.2(–10.6) μm in diameter, ornamented with uniformly distributed bacula, of varying sizes (visible under LM), widened at the top (SEM, all except the smallest ones), secondary ornamentation ranges from rough to very finely verrucous. Plasmodium not observed.

Additional materials examined: RUSSIA, Murmansk Region, Monchegorsk Municipal District, Laplandskiy State Nature Biosphere Reserve, 67.6838° N, 32.3646° E, on decayed wood of *Picea obovata*, 26 Aug 2015, field, leg. Novozhilov Yu.K., Shchepin O.N., Erastova D.A., and Tikhonova E.N. (LE306548).

Distribution: currently known from European Russia (Murmansk Region).

Habitat: on rotten coniferous wood.

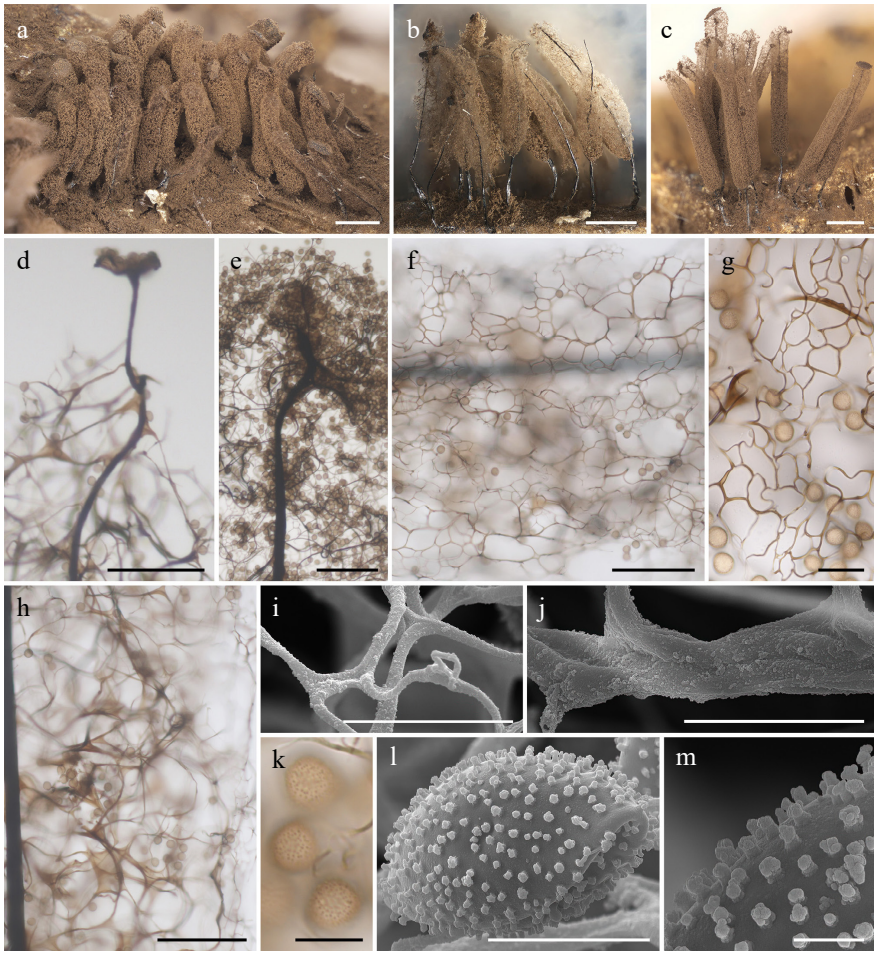

Fig. 2 Morphological characteristics of *Corallosporopsis gabrieliana* (a), (b), (d), (f), (h)–(j), (l), (m) LE306548; (c), (e), (g), (k). LE306833. (a)–(c) Mature sporocarps (DM). (d), (e) Apical view of the sporotheca (LM). (f), (g) Surface net (LM). (h) Capillitium in the middle part of the sporotheca (LM). (i) Detail of the surface net (SEM). (j) Detail of the capillitium threads (SEM). (k) Spores (LM). (l) Spore (SEM). (m) Detail of the spore ornamentation (SEM). Scale bars: (a)–(c) = 1 mm; (d)–(f), (h) = 100 μm; (g) = 20 μm; (i)–(k) = 10 μm; (l) = 5 μm; (m) = 1 μm.

Notes: Two specimens from this clade were previously reported as the first Russian records of *Cor. capillitionodosa*[69,70]. While they share key characteristics of that species, a funnel-shaped expansion at the columella apex, triangular flattened expansions in the internal capillitium, and coral-like warts on spores 9–11 μm in diameter[68], both geography and morphology support their recognition as a distinct species.

Geographically, *Cor. capillitionodosa* is described from Central America, whereas these two specimens originate from the boreal zone of European Russia. Morphologically, they differ in having a wider sporotheca (0.3–0.6 mm vs 0.10–0.25 mm in *Cor. capillitionodosa*) and a denser surface net with smaller meshes. Although Vlasenko et al.[69] reported that the surface net meshes of these two specimens can reach 130 μm, a value matching the range given in the protologue of *Cor. capillitionodosa*[68], a re-examination conducted in the present study found no meshes exceeding 76 μm in diameter. Another related species, *Cor. flavogenita*, differs in its generally larger sporocarps, 5.5 mm in total height or even up to 8 mm in total height, and smaller spores 7–9.5 μm in diameter[71].

The Russian materials are described as the new species *Cor. gabrieliana*. Given the current ambiguity surrounding the precise application of recombined names in *Corallosporopsis* (see Notes on *Cor. flavogenita* and *Cor. herbatica*), *Cor. gabrieliana* is designated as the type of *Corallosporopsis*. This ensures a stable nomenclatural anchor linked to a molecularly characterized specimen.

***Corallosporopsis gracilis* (G. Lister) Bortnikov, W.L. Song & Novozh., comb. nov.**

MycoBank number: MB863316.

Basionym: *Comatricha pulchella* var. *gracilis* G. Lister, A monograph of the Mycetozoa: 156 (1911).

Synonym: *Stemonitopsis gracilis* (G. Lister) Nann.-Bremek., De Nederlandse Myxomyceten: 21 (1975).

Materials examined: RUSSIA, Jewish Autonomous Region, Obluchensky District, Bastak Nature Reserve, 49.0691° N, 133.0739° E, on decayed wood of *Maackia amurensis*, 30 Jun 2022, field, leg. Bortnikov F.M. (LE348922); Primorye Territory, Vladivostok Urban Okrug, Botanical Garden Institute, 43.2200° N, 131.9950° E, on bark of living *Abies holophylla*, 10 Feb 2022, moist chamber, leg. Bortnikov F.M. (MYX 22279).

Notes: *Stemonitopsis gracilis* is morphologically similar to *Cor. pulchella* (a variety of which was originally described) but differs in several respects, including a shorter stalk, narrower cylindrical sporotheca, distinct stalk and columella structures, the presence of a surface net, and smaller meshes in the internal capillitium net near the sporotheca periphery[76].

It also resembles *Stemonitopsis subcaespitosa* (Peck) Nann.-Bremek. but can be distinguished by its denser, more sinuous surface net and smaller spores: 5–7 μm[23] vs 7–10 μm[13], and 9–10 μm from the type specimen of *Stp. subcaespitosa*[77]. Additionally, the spores of *Stp. subcaespitosa* bear bacula that lack expanded tips (see Moreno et al.[77]: figs 56–59).

The *Cor.* cf. *gracilis* specimens examined in this study (LE348922, field-collected; MYX 22279, moist chamber; both from the Russian Far East) show some minor variation in sporotheca thickness (0.43 mm vs 0.30 mm in diameter) and spore size (on average 7.8–8.3 μm vs 6.9–7.5 μm in diameter). Overall, they are similar to each other and correspond well to the concept of *Cor. gracilis*, differing only in slightly larger spores (5.6–7.0 μm in the protologue)[79].

***Corallosporopsis herbatica* (Peck) W.L. Song, Bortnikov, Shuang L. Chen & Novozh., comb. nov. Figs 3, 4**

MycoBank number: MB863317.

Basionym: *Stemonitis herbatica* Peck, Bull. Buffalo Soc. Nat. Sci. 1 (6-9): 64 (1873).

Materials examined: CHINA, Qinghai Province, Haile City, Ledu District, 36.3000° N, 102.2200° E, on leaves, 12 Jul 2004, field, leg. Zhang X.Q., Guo L., and Li W. (HMAS 98461); Zhejiang Province, Hangzhou City, Tianmu Mountain National Nature Reserve, 30.3477° N, 119.4439° E, on leaves, 19 Oct 2012, field, leg. Liu Q.S. (HFNNU 12495). **RUSSIA,** Jewish Autonomous Region, Obluchensky District, Bastak Nature Reserve, 49.0691° N, 133.0739° E, on deciduous litter, 30 Jun 2022, field, leg. Bortnikova N.A. (LE348810).

Note: *Stemonitis herbatica* was initially briefly described from the USA[80], with a more complete morphological description and illustrated by Lister[79]. This species is characterized by densely gregarious sporocarps forming small clusters on leaf litter, 5–9 mm in total height, a short stalk (Figs 3a; 4a–c), a capillitium that forms an internal net with nodules and a dense surface net of pale, non-spiny meshes (Figs 3f, g; 4g, h), and spores measuring 7–8.9(–9) μm in diameter with distinctive warts[71,79]. Examination of a putative isotype by Moreno et al.[71] revealed that the bacula on the spore surface possess distinct apical thickenings (see Moreno et al.[71]: fig. 6d–f), supporting the transfer of this species to *Corallosporopsis* as *Cor. herbatica*.

The examination of three specimens (HMAS 98461, HFNNU 12495, and LE348810) further supports this reclassification. These specimens correspond closely to the description of Lister[79] and Moreno et al.[71] in all key morphological characteristics, including growth habit, sporocarp dimensions, surface net structure (Fig. 3f, g), and spore diameter and ornamentation. Minor variations were observed: in the Chinese specimens (HMAS 98461 and HFNNU 12495), capillitial branches occasionally ran nearly parallel to the columella (Fig. 3e, i, j), and the bacula on the spores are more densely distributed (Fig. 3l, m) than in the putative isotype (see Moreno et al.[71]: fig. 6d–f). Importantly, the diagnostic apical thickening of the bacula is also present in the examined specimens (Figs 3m, 4m).

In the three-gene phylogenetic tree, all three *Cor. herbatica* specimens are placed within the *Corallosporopsis* clade (Fig. 1), strongly justifying the transfer. However, they form two distinct subclades that are intermixed with *Cor. pallida* (≡ *Ste. pallida*) HK0208033 and *Stemonitis lignicola* BW0545. In the absence of molecular data from samples originating from the type locality (the East Coast of the USA), it is not possible to determine definitively which lineage, the Chinese specimens or those from the Russian Far East and Europe, represents the 'true' *Cor. herbatica*. See also Notes on *Cor. flavogenita*.

***Corallosporopsis laxifila* (Nann.-Bremek. & Y. Yamam.) W.L. Song, Bortnikov, Shuang L. Chen & Novozh., comb. nov. Fig. 5**

MycoBank number: MB863318.

Basionym: *Stemonitis laxifila* Nann.-Bremek. & Y. Yamam., Watanabe & Malla (eds.), Crypt. Himalayas, vol. 1: 29 (1988).

Materials examined: NEPAL, Bagmati Province, Kathmandu District, Swayambhu, on mossy bark, 31 Aug 1986, field, leg. Watanabe M. (holotype, TNS-M-H-4376 = YY-4814).

Notes: *Stemonitis laxifila* was first described from Nepal[81] and has rarely been reported since. Examination of the holotype (TNS-M-H-4376 = YY-4814; Fig. 5) in this study revealed it to be in poor condition due to age: spores are scarce and seldom aggregated, and slight fungal contamination precluded successful DNA extraction and sequencing. New measurements of the holotype are as follows: sporocarps 1.6–2.0(–2.1) mm in total height, (0.1–)0.2–0.3 mm in width; stalk 0.2–0.6(–0.9) mm long (25%–50% of the total height); and spores (8.5–)9.1–9.9(–10.3) μm in diameter. These values largely correspond to the original description (sporocarps ca. 2.5 mm in total height, 0.25–0.3 mm wide, stalk about 1/3 or slightly more of

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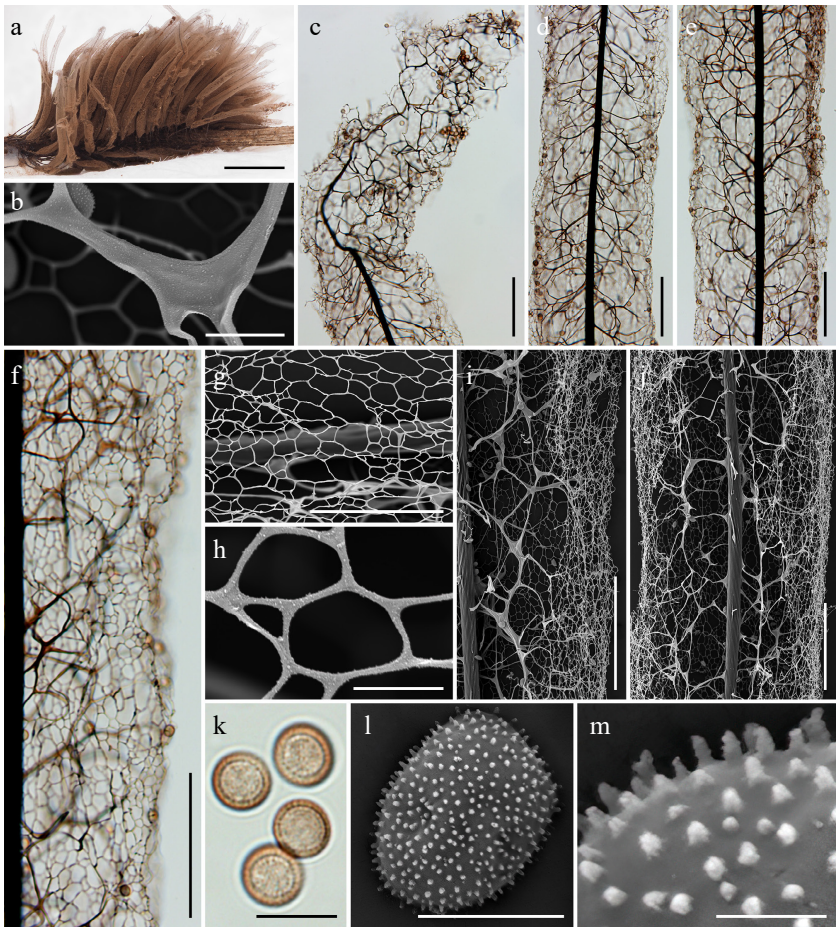

Fig. 3 Morphological characteristics of *Corallosporopsis herbatica* (HMAS 98461). (a) Mature sporocarps (DM). (b) Detail of the capillitium threads (SEM). (c) Apical view of the sporotheca (LM). (d), (e) Capillitium in the middle part of the sporotheca (LM). (f) Surface net (LM). (g), (h) Detail of the surface net (SEM). (i), (j) Capillitium in the middle part of the sporotheca (SEM). (k) Spores (LM). (l) Spore (SEM). (m) Detail of the spore ornamentation (SEM). Scale bars: (a) = 2 mm; (c)–(f), (i), (j) = 100 μm; (b), (g), (k) = 10 μm; (h), (l) = 5 μm; (m) = 1 μm.

the total height, and spores 7–8 × 9–10 μm in diameter). Detailed morphological study revealed several previously undescribed characteristics: the capillitium threads are nearly smooth (Fig. 5j); the surface net is loose and irregular, with large meshes (Fig. 5i); and the spore ornamentation consists of bacula with distinct apical thickening (Fig. 5l, m). The characteristic apical thickening of the bacula supports the placement of this species within *Corallosporopsis* as defined in this study for taxa sharing this characteristic. Therefore, *Ste. laxifila* is transferred to *Corallosporopsis* as *Cor. laxifila*.

***Corallosporopsis mediterraneensis* (H.H. Doğan & Eroğlu) Gmoshinskiy, W.L. Song & Bortnikov, comb. nov.**

MycoBank number: MB863319.

Basionym: *Stemonitis mediterraneensis* H.H. Doğan & Eroğlu, Mycotaxon 129 (2): 294 (2015).

Notes: *Stemonitis mediterraneensis* was described from Turkey[82], where it was found on rotten wood of *Abies cilicica*. This species is characterized by pale brown, stalked sporocarps, 2.2–3.5 mm in total height, 0.2–0.4 mm in diameter, and large spores measuring (8.5–)9–10.6 μm in diameter. SEM images of the spores (see Doğan & Eroğlu[82]: fig. 1E, F) show that bacula possess distinct apical thickening. This characteristic aligns with the diagnosis of *Corallosporopsis*. Therefore, *Ste. mediterraneensis* is transferred to *Corallosporopsis* as *Cor. mediterraneensis*.

***Corallosporopsis pallida* (Wingate) Bortnikov, W.L. Song & Novozh., comb. nov.**

MycoBank number: MB863321.

Basionym: *Stemonitis pallida* Wingate, The North American slime-moulds: 123 (1899).

Notes: *Stemonitis pallida* was described from Pennsylvania, USA[83]. Examination of the type specimen[71] revealed that the bacula on the spore surface possess apically thickened tips (see Moreno et al.[71]: fig. 8h) characteristic of *Corallosporopsis*, justifying the transfer proposed in this study as *Cor. pallida*.

The species is characterized by light-brown sporocarps, 2–6 mm in total height, spores 6–7.7 μm in diameter with individual discernible spines under a 100× oil immersion objective[71] and a tendency to form a complete surface net with numerous pointed free ends. The columella apex is sometimes greatly expanded, approaching the condition seen in *Cor. flavogenita*, though the latter typically has a more pronounced expansion and a coarser, darker capillitium[72]. *Corallosporopsis herbatica* differs in its large spores (7–9 μm in diameter) with more pronounced warts and the absence of spiny outgrowths on the surface net.

In the phylogenetic analysis conducted in this study, the single specimen of *Cor. pallida* (HK0208033) groups closely with *Stemonitis lignicola* BW0545 and a specimen LE348810 identified in this study as *Cor.* cf. *herbatica* (Fig. 1), suggesting they may be conspecific. However, as the first two specimens were not available for morphological verification, their identifications remain tentative. Thus, while morphological evidence strongly supports the placement of *Ste. pallida* in *Corallosporopsis*, its precise phylogenetic position requires further clarification.

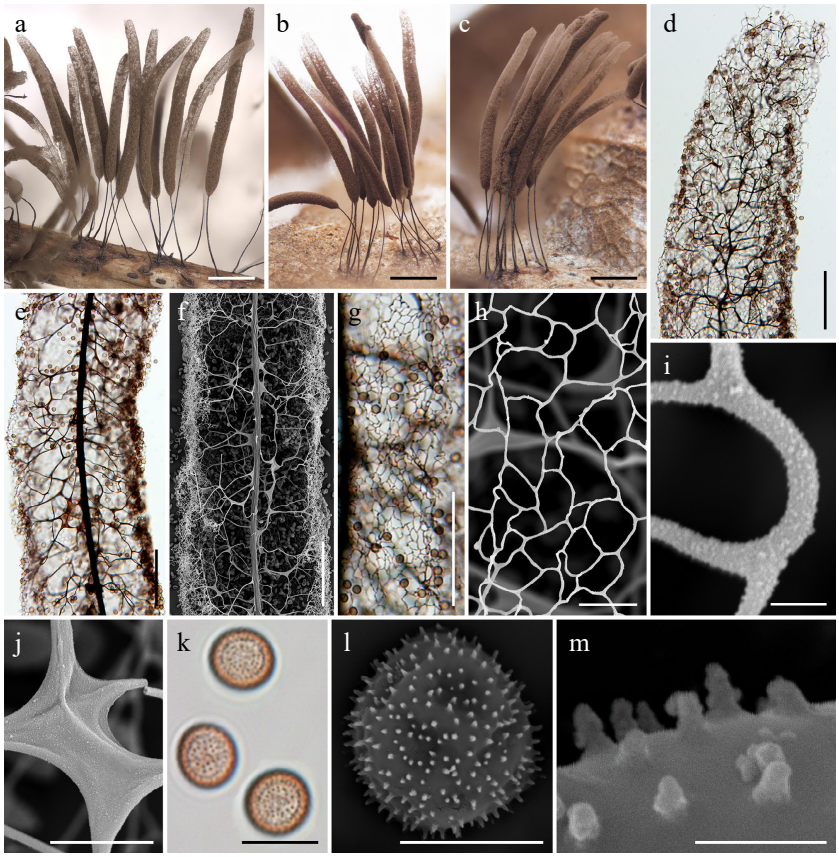

Fig. 4 Morphological characteristics of *Corallosporopsis herbatica* (LE348810). (a)–(c) Mature sporocarps (DM). (d) Apical view of the sporotheca (LM). (e) Capillitium in the middle part of the sporotheca (LM). (f) Capillitium in the middle part of the sporotheca (SEM). (g) Surface net (LM). (h), (i) Detail of the surface net (SEM). (j) Detail of the capillitium threads (SEM). (k) Spores (LM). (l) Spore (SEM). (m) Detail of the spore ornamentation (SEM). Scale bars: (a)–(c) = 1 mm; (d)–(g) = 100 μm; (h), (j), (k) = 10 μm; (l) = 5 μm; (i), (m) = 1 μm.

***Corallosporopsis pallidofila* (Y. Yamam. & Nann.-Bremek.) W.L. Song, Bortnikov, Shuang L. Chen & Novozh., comb. nov. Fig. 6**

MycoBank number: MB863322.

Basionym: *Stemonaria pallidofila* Y. Yamam. & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C 93: 278 (1990).

Materials examined: JAPAN, Kochi Prefecture, Nankoku City, Kureta, on bark of dead *Hibiscus syriacus*, 23 Jul 1989, field, leg. Yamamoto Y. (holotype, TNS-M-Y-22050 = YY-8346).

Notes: *Stemonaria pallidofila* was described from Japan[84] and has rarely been reported since. Examination of the holotype (TNS-M-Y 22050: Fig. 6) revealed it to be in poor condition due to its age and heavy fungal contamination, which precluded DNA extraction and sequencing. New measurements of the holotype are as follows: sporocarps (1.0–)1.2–1.8(–2.1) mm in total height, 0.2 mm in width; stalk (0.3–)0.4–0.6(–0.7) mm long (18%–50% of the total height); spores (9.8–)10.6–11.2(–11.9) μm in diameter. These data largely align with the original description, which reported sporocarps 1.2–2 mm in total height, 0.25–0.3 mm wide, a stalk about 1/3–1/2 of the total height, and spores 10–11 μm in diameter[84]. Detailed morphological study shows that the species sometimes bears a very delicate, highly irregular, and often incomplete surface net (Fig. 6k). The capillitial threads are minutely warted (Fig. 6l). Spores are ornamented with irregularly distributed bacula with distinct apical thickening (Fig. 6n, o), accompanied by irregularly scattered small warts (Fig. 6p). The presence of apically thickened bacula aligns with the diagnostic characteristic of *Corallosporopsis*. Therefore, *Sta. pallidofila* is transferred to *Corallosporopsis* as *Cor. pallidofila*.

***Corallosporopsis pulchella* (C. Bab.) Bortnikov, W.L. Song & Novozh., comb. nov.**

MycoBank number: MB863320.

Basionym: *Stemonitis pulchella* C. Bab., Proceedings of the Linnean Society, London: 32 (1839).

Synonym: *Comatricha pulchella* (C. Bab.) Rostaf., Sluzowce Monografia, Appendix: 27 (1876).

Synonym: *Comatricha persoonii* var. *fusca* Lister, J. Bot., London: 215 (1879).

Notes: *Comatricha pulchella* has small sporocarps up to 1.5(–3) mm in total height, developing on litter or, less commonly, on decaying wood[13]. Its spores are 6.5–8 μm in diameter and spiny. Under SEM, the bacula are sparse and have distinct apical thickenings (see Moreno et al.[85]: fig. 7; Moreno et al.[86]: figs 1, 2). The latter characteristic is diagnostic for *Corallosporopsis*, and therefore the new combination *Cor. pulchella* is proposed.

This spore ornamentation was further confirmed by the examination of the syntype of *Com. persoonii* var. *fusca* (= *Com. pulchella*), which verified that it is a synonym of *Cor. pulchella*[59]. *Comatricha pulchella* var. *gracilis*, currently recognized as the separate species *Stp. gracilis*, is also transferred to *Corallosporopsis* in this study (see notes above).

***Corallosporopsis spinispora* (Novozh. & D.W. Mitch.) Bortnikov, Gmoshinskiy, W.L. Song & Novozh., comb. nov.**

MycoBank number: MB863323.

Basionym: *Comatricha spinispora* Novozh. & D.W. Mitch., Novosti Sist. Nizsh. Rast. 48: 191 (2014).

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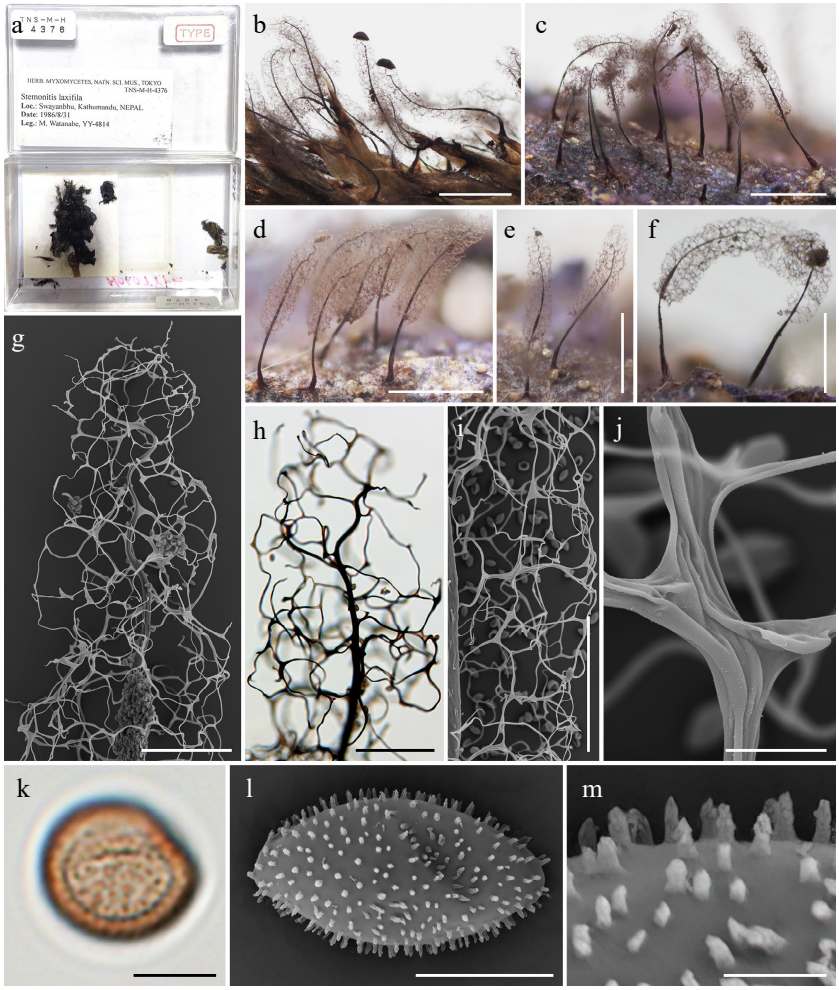

Fig. 5 Morphological characteristics of the holotype (TNS-M-H-4376 = YY-4814) of *Corallosporopsis laxifila* (≡ *Stemonitis laxifila*). (a) Herbarium labels and interior views of the herbarium box containing the holotype. (b)–(f) Mature sporocarps (DM). (g) Apical view of the sporotheca (SEM). (h) Apical view of the sporotheca (LM). (i) Capillitium in the middle part of the sporotheca (SEM). (j) Detail of the capillitium threads (SEM). (k) Spore (LM). (l) Spore (SEM). (m) Detail of the spore ornamentation (SEM). Scale bars: (b)–(f) = 1 mm; (g)–(i) = 100 μm; (j) = 10 μm; (k), (l) = 5 μm; (m) = 1 μm.

Materials examined: VIETNAM, Dong Nai Province, Tan Phu District, Cat Tien National Park, 11.4404° N, 107.3996° E, on leaf litter, 28 Mar 2013, moist chamber (pH = 4.62), leg. Novozhilov Yu.K. (LE297432).

Notes: *Comatricha spinispora* was described based on specimens from Vietnam[87]. The species is distinguished by its distinctive spore ornamentation: long spines 0.5–0.8 μm in length, with 6–8 very small additional spines (0.1–0.3 μm long) densely distributed over the upper part of each main spine, visible only under SEM (see Novozhilov & Mitchell[87]: Pl. Ig, i). This morphology aligns with the diagnostic characteristic of *Corallosporopsis*. Therefore, *Com. spinispora* is transferred to *Corallosporopsis* as *Cor. spinispora*. This recombination is supported by the molecular phylogeny of Shchepin et al.[88], in which the sequence of *Cor. spinispora* is placed within the *Stemonitis* s. lat. 1 clade corresponding to the *Corallosporopsis* clade in the present study.

• *Grandiverruca* W.L. Song, Bortnikov, Gmoshinskiy, Shuang L. Chen & Novozh., gen. nov.

MycoBank number: MB863076.

Etymology: from the Latin *grandis* (large) and *verruca* (wart), referring to the large, irregularly dispersed verrucae of the spore ornamentation, which is a diagnostic characteristic of the genus.

Type (designated here): *Grandiverruca verrucosifila* W.L. Song & Shuang L. Chen.

Diagnosis: Sporocarps stalked, relatively densely gregarious; spores orange-brown to pale brown, relatively small (mostly less than 6 μm), with an unevenly thickened wall, ornamented with large and irregularly arranged verrucae pale to inconspicuous in LM and clearly visible under SEM.

Description: Sporocarps densely gregarious, in small clusters or groups, small, ca. 2–6 mm in total height. Sporotheca mostly orange-brown. Stalk conspicuous, not exceeding 50% of the total height. Columella tapering upwards, filamentous and unbranched at the sporotheca apex, without expansion. Capillitium dense, often sinuous, with irregular membranous expansions at the branching points, threads bearing conspicuous, irregular small warts. Surface net complete, with distinct meshes, threads bearing conspicuous small warts. Spores small, with an unevenly thickened wall, ornamented with large and irregularly arranged verrucae, sometimes interspersed with irregular small warts.

Accepted species: *Grandiverruca smithii* (T. Macbr.) Gmoshinskiy, Bortnikov & W.L. Song, and *G. verrucosifila* W.L. Song & Shuang L. Chen.

Notes: The primary diagnostic characteristic of *Grandiverruca* is the combination of relatively small sporocarps and spores ornamented with large, globose verrucae visible under SEM. While this

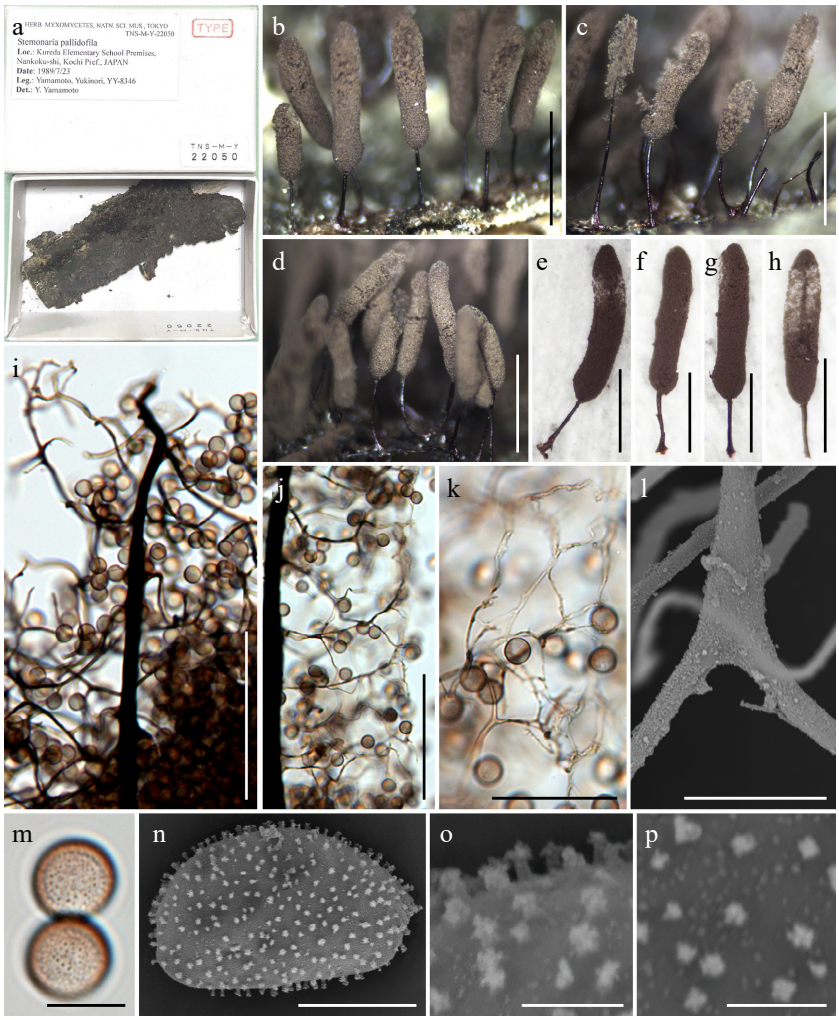

Fig. 6 Morphological characteristics of the holotype (TNS-M-Y-22050 = YY-8346) of *Corallosporopsis pallidofila* (≡ *Stemonaria pallidofila*). (a) Herbarium labels and interior views of the herbarium box containing the holotype. (b)–(h) Mature sporocarps (DM). (i) Apical view of the sporotheca (LM). (j) Capillitium in the middle part of the sporotheca (LM). (k) Surface net (LM). (l) Detail of the capillitium threads (SEM). (m) Spores (LM). (n) Spore (SEM). (o), (p) Detail of the spore ornamentation (SEM). Scale bars: (b)–(h) = 1 mm; (i), (j) = 100 μm; (k) = 50 μm; (l), (m) = 10 μm; (n) = 5 μm; (o), (p) = 1 μm.

ornamentation type appears distinctive within the Stemonitidales, its reliable observation depends on SEM. In the absence of detailed SEM data from the types of other potentially allied species, this study refrains from proposing further transfers to *Grandiverruca* at this time.

Phylogenetically, the type *G. verrucosifila* and the taxon treated here as *G.* cf. *smithii* (see below) form a well-supported monophyletic clade (UBS/PP/TBE = 100/100/100; Fig. 1). This clade is sister to *Stemonitis* s.str., confirming the distinct and independent status of *Grandiverruca*.

***Grandiverruca smithii* (T. Macbr.) Gmoshinskiy, Bortnikov & W.L. Song, comb. nov. Fig. 7**

MycoBank number: MB863324.

Basionym: *Stemonitis smithii* T. Macbr., Bull. Iowa Univ. Lab. Nat. Hist. 2(4):381 (1893).

Materials examined: RUSSIA, Moscow, Serpukhov, Prioksko-Terrasnyi Natural State reserve, 54.8638° N, 37.6310° E, on rotten wood, 5 Jul 2022, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 20613); Primorye Territory, Khasansky District, Kedrovaya Pad Nature Reserve, 43.1649° N, 131.4744° E, on decayed deciduous wood, 14 Jul 2020, field, leg. Bortnikova N.A. (LE327934); Leningrad Region, Vyborgsky District, Bolshoy Beryozovy Island, 60.2919° N, 28.6881° E, on a log of *Alnus nigra*, 18 Sep 2024, field, leg. Novozhilov Yu.K. and Luptakova A.D. (LE347064).

Description: Sporocarps erect, stalked, densely to loosely gregarious in small groups, (3.0–)3.2–3.6(–3.8) mm in total height. Sporotheca cylindrical or slightly tapering downwards, apex bluntly rounded, brown with orange, 0.2–0.3 mm wide. Stalk black, shiny, 1.0–1.2 mm long, 25%–38% of the total height, base expanded into a triangular shape. Hypothallus membranous, silvery white or inconspicuous, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex, unbranched. Capillitium arising perpendicularly from the entire length of the columella, dense, sinuous, strong brown to deep orange, with a triangular membranous expansion at the point of origin, highly and intricately branched, with irregular, paler membranous expansions at the branching points, threads ornamented with small warts, connecting to the surface net. Surface net well-developed, often slightly incomplete at the sporotheca apex but complete elsewhere; threads filamentous to flattened-band-shaped, slightly sinuous, forming irregularly polygonal to subcircular meshes, (8–)25–54(–85) μm in diameter; threads ornamented with irregular warts and sparsely bearing spines of variable length. Spore concolorous with the sporotheca in mass, pale brown in transmitted light, globose to subglobose, (4.1–)4.5–4.8(–5.8) μm in

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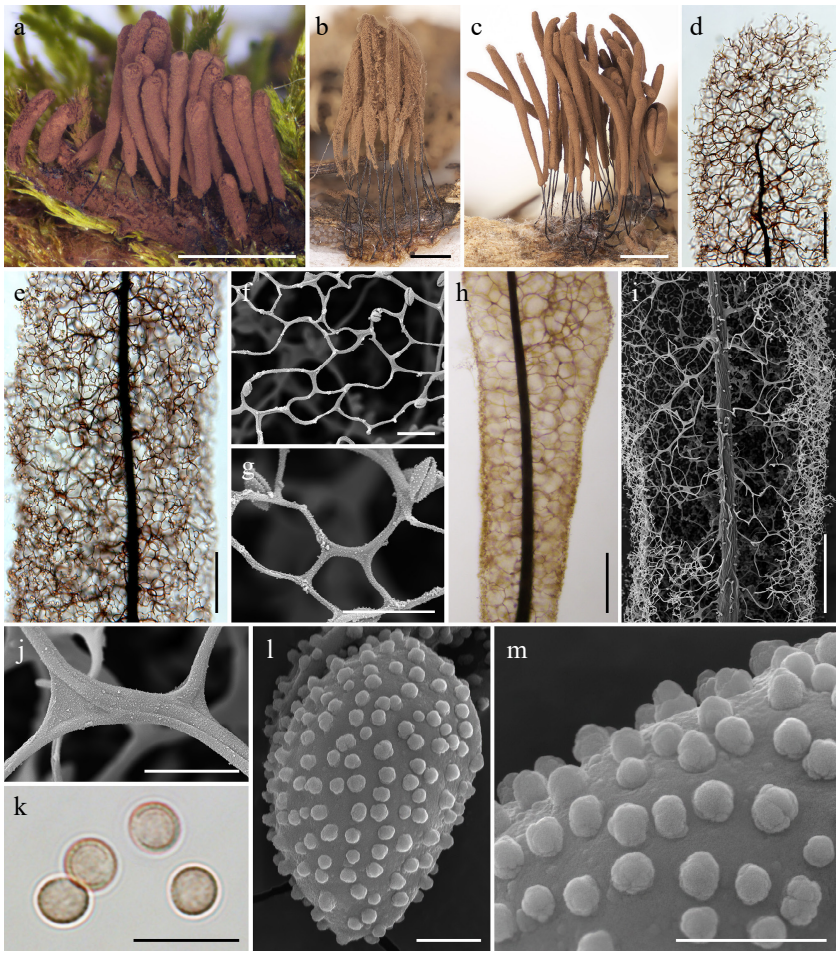

Fig. 7 Morphological characteristics of *Grandiverruca* cf. *smithii* (a), (h) MYX 20613; (b), (d)–(g), (i)–(m) LE327934; (c) LE347064. (a)–(c) Mature sporocarps (DM). (d) Apical view of the sporotheca (LM). (e) Surface net (LM). (f), (g) Detail of the surface net (SEM). (h) Capillitium in the middle part of the sporotheca (LM). (i) Capillitium in the middle part of the sporotheca (SEM). (j) Detail of the capillitium threads (SEM). (k) Spores (LM). (l) Spore (SEM). (m) Detail of the spore ornamentation (SEM). Scale bars: (a) = 2 mm; (b), (c) = 1 mm; (d), (e), (h), (i) = 100 μm; (f), (g), (j), (k) = 10 μm; (l), (m) = 1 μm.

diameter, ornamented with large and irregular verrucae unevenly dispersed, sometimes interspersed with irregular small warts. Plasmodium not observed.

Notes: *Stemonitis smithii* is currently treated as a synonym of *Sym. ferrugineus* (a new combination proposed in this study for *Stemonitis ferruginea* Ehrenb.)[71], a conclusion not based on examination of the type material of *Ste. smithii*[89]. The protologue of *Ste. smithii*[83] reports spores 4–5 μm in diameter, later amended to 4–7 μm[83], and subsequently to a narrower range (up to 6 μm)[76]. Moreno et al.[71] considered the minimal spore size difference from *Sym. ferrugineus* to be only 0.5 μm and noted that specimen 'Rex 51' (identified as *Ste. smithii*) exhibited the characteristic minute reticulum between warts of *Sym. ferrugineus*. Nevertheless, the sporocarps of *Ste. smithii* and *Sym. ferrugineus* differ significantly. Therefore, given that 1) according to the present results, all *Sym. ferrugineus* specimens with large sporocarps occupy a distantly related phylogenetic position within *Symphytocarpus* (Fig. 1); 2) Macbride's morphological observations on *Stemonitis castillensis* T. Macbr., another species described from Nicaragua at the same time as *Ste. smithii*[83], have been well confirmed in this study on specimens from Brazil; 3) the type material of *Ste. smithii*, or at least geographically comparable material, remains underexamined, the differences between *Ste. smithii* and *Sym. ferrugineus* justify considering them as separate species. Consequently, in this study, *Ste. smithii* continues to be recognized as an independent species.

Three specimens (MYX 20613, LE327934, LE347064) examined in this study are morphologically very similar to *Ste. smithii*, particularly sharing small sporocarps and spores[89]. However, they exhibit some minor morphological differences from the protologue of *Ste. smithii*. The sporocarps of the examined material measure (3.0–)3.2–3.6(–3.8) mm in total height, which is slightly larger than those of *Ste. smithii* (ca. 2.5 mm). Furthermore, the capillitium of these specimens is somewhat denser, and the stalk constitutes 25%–38% of the total height (Fig. 7a–c). This contrasts with the protologue of *Ste. smithii*, where the stalk and sporotheca are described as subequal (ca. 50%). Without examining the type material of *Ste. smithii*, these minor differences are insufficient to support these three specimens as a new, independent species.

Phylogenetically, these three specimens form a well-supported sister group (UBS/PP/TBE = 100/100/100; Fig. 1) with *G. verrucosifila*, the type of the newly described genus *Grandiverruca* in this study. These specimens clearly differ from *G. verrucosifila*, which has larger sporocarps ([3.7–]4.2–4.5[–5.0] mm in total height), distinctly smaller and denser surface net meshes ([9–]16–25[–43] μm in diameter), and a simpler capillitium. The phylogenetic results indicate that these three specimens belong to *Grandiverruca*. Given their high morphological similarity to *Ste. smithii*, it is concluded that *Ste. smithii* should also be placed in this genus. Therefore, *Ste. smithii* is formally transferred to *Grandiverruca* as *G. smithii*. However, since the type material of *G. smithii* was not examined, these specimens

cannot be definitively identified as this species. Because they cannot be described as a new species based on the current minor differences, these three studied specimens are annotated as *G.* cf. *smithii*.

***Grandiverruca verrucosifila* W.L. Song & Shuang L. Chen, sp. nov.** **Fig. 8**

MycoBank number: MB863081.

Etymology: *verrucosifila* (Latin) with warty or roughened threads, from *verru* (wart, from *verruca*) and *filis* (thread, from *filum*) referring to the threads of the surface net which are densely covered with small, conspicuous, wart-like ornamentations.

Holotype: CHINA, Anhui Province, Suzhou City, Huangzangyu National Forest Park, 34.0253° N, 117.0573° E, on rotten wood, 19 Aug 2023, field, leg. Song W.L. and Rao G. (HFNNU 9746, GenBank *nrSSU*: PZ106604; *EF-1α*: PZ163032; *mtSSU*: PZ160606).

Diagnosis: Sporocarps densely gregarious, (3.7–)4.2–4.5(–5.0) mm in total height; stalk shorter (14%–36% of the total height); surface net with larger meshes (9–)16–26(–43) μm in diameter, spores (3.7–)4.4–5.3(–6.0) μm in diameter, ornamented with large and irregular verrucose processes unevenly dispersed, sometimes interspersed with irregular small warts.

Description: Sporocarps erect, stalked, densely gregarious, (3.7–)4.2–4.5(–5.0) mm in total height. Sporotheca elongate-cylindrical, tapering towards both ends, apex bluntly rounded, brown to brownish orange, 0.2–0.3 mm wide. Stalk black, shiny, (0.6–)0.8–1.3(–1.5) mm long, 14%–36% of the total height, base forming a short cone. Hypothallus membranous, moderate orange to light orange, shiny, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex as a slender filament, unbranched. Capillitium arising from the entire length of the columella, dense, deep orange to brownish orange, with a triangular expansion at the point of origin, much and intricately branched, with irregular membranous expansions at the branching points, threads densely covered with small warts, connecting to the surface net. Surface net well-developed, often slightly incomplete at the sporotheca apex but complete elsewhere; threads slightly undulate, meshes of unequal diameter, (9–)16–25(–43) μm in diameter, densely covered with irregular small warts, sparsely bearing spines of variable length. Spore concolorous with the sporotheca in mass, pale brown in transmitted light, globose to subglobose, (3.7–)4.4–5.3(–6.0) μm in diameter, ornamented with large and irregular verrucose processes unevenly dispersed, sometimes interspersed with irregular small warts. Plasmodium not observed.

Additional materials examined: CHINA, Anhui Province, Suzhou City, Huangzangyu National Forest Park, 34.0234° N, 117.0555° E, on

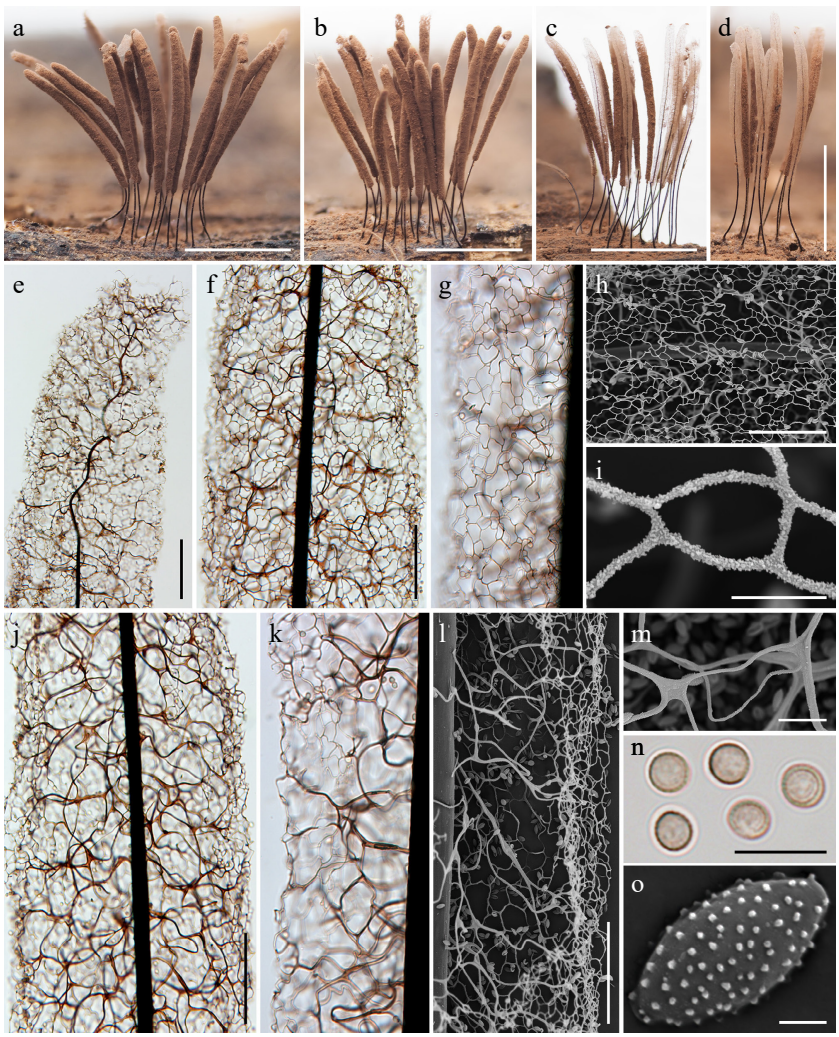

Fig. 8 Morphological characteristics of *Grandiverruca verrucosifila* (a), (b), (e), (m), (o) HFNNU 9746; (c), (d), (f), (j), (n) HFNNU 4477; (g)–(i), (k), (l) HFNNU 10346. (a)–(d) Mature sporocarps (DM). (e) Apical region of the sporocarp (LM). (f), (g) Surface net (LM). (h), (i) Detail of the surface net (SEM). (j), (k) Capillitium in the middle part of the sporotheca (LM). (l) Capillitium in the middle part of the sporotheca (SEM). (m) Detail of the capillitium threads (SEM). (n) Spores (LM). (o) Spore (SEM). Scale bars: (a)–(d) = 2 mm; (e), (f), (j) = 100 μm; (g), (h), (k), (l) = 50 μm; (m), (n) = 10 μm; (i), (o) = 5 μm.

rotten wood, 19 Aug 2023, field, leg. Song W.L. and Rao G. (HFNNU 4477); Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, 32.0626° N, 118.8641° E, on rotten wood, 19 Jul 2022, field, leg. Lin D. (HFNNU 10346); Henan Province, Nanyang City, Baotianman National Nature Reserve, 33.4719° N, 111.9623° E, on rotten wood, 25 Sep 2016, field, leg. Gao Y. and Wang G.W. (HFNNU 13265).

Distribution: currently known from Central and Eastern China.

Habitat: on rotten wood.

Notes: Morphologically, *G. verrucosifila* is similar to *G. smithii* in sporocarp and spore size. However, it differs in several key characteristics: *G. verrucosifila* has larger sporocarps measuring (3.7–)4.2–4.5(–5.0) mm in total height vs ca. 2.5 mm in *G. smithii*], a shorter stalk (14%–36% of the total height vs ca. 50% in *G. smithii*), and surface net meshes that are significantly larger than its spore diameter, whereas in *G. smithii* the net meshes are approximately equal to the spore size[89]. Although *G. smithii* is currently treated as a synonym of *Sym. ferrugineus* prior to this study, *G. verrucosifila* is distinct. Its spore ornamentation consists only of large, irregular verrucae processes unevenly dispersed, sometimes interspersed with small warts (Fig. 8n, o) and completely lacks the secondary reticulum characteristic of *Sym. ferrugineus*[71]. The spores are also distinctly smaller, measuring (3.7–)4.4–5.3(–6.0) μm in diameter, than those of the *Sym. ferrugineus* isotype (5.3–6.7[–7.0] μm in diameter). Furthermore, the surface net of *G. verrucosifila* has larger, more variable meshes and threads that are more densely warted and bear spines (Fig. 8f–i), unlike the finer, less ornamented net of *Sym. ferrugineus*[71].

Phylogenetic analysis supports this distinction: in the three-gene phylogenetic tree, *G. verrucosifila* forms an independent, well-supported clade closely related to *G.* cf. *smithii* (UBS/PP/TBE = 100/100/100; Fig. 1). Based on this combination of unique morphological characteristics and molecular evidence, *G. verrucosifila* is described as a new species.

[*Stemonaria* Nann.-Bremek., R. Sharma & Y. Yamam.]

MycoBank number: MB25011.

Type: *Stemonaria fuscoides* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 87: 460 (1984) (≡ *Stemonitis fuscoides* (Nann.-Bremek. & Y. Yamam.) Shchepin, Prikhodko, Gmoshinskiy, Schnittler & Novozh.).

Temporarily formally recognized species: *Stemonaria argentella* Y. Yamam., *Sta. clausifila* Nann.-Bremek. & Y. Yamam., *Sta. laxa* Nann.-Bremek. & Y. Yamam., *Sta. laxiretis* Nann.-Bremek. & Y. Yamam., and *Sta. rufipes* Nann.-Bremek. & Y. Yamam.

Notes: Sixteen species have been recognized in *Stemonaria*[6]. However, the genus *Stemonaria* must be disbanded because its type, *Sta. fuscoides*, possesses warted-reticulate spores and has been transferred to *Stemonitis* s.str. as *Ste. fuscoides*, a name that takes priority[88]. In addition, *Sta. fuscoides* Nann.-Bremek. & Y. Yamam., *Sta. gracilis* Nann.-Bremek. & Y. Yamam., and *Sta. longa* (Peck) Nann.-Bremek., R. Sharma & Y. Yamam. were formally transferred or resurrected to *Stemonitis* s.str.[88]. In the present study, new combinations are proposed for four further species and are transferred as follows: *Sta. liaoningensis* B. Zhang & Yu Li, *Sta. minuta* Nann.-Bremek. & Y. Yamam., and *Sta. pilosa* Nann.-Bremek. to *Stemonitis* s.str.; and *Sta. pallidofila* Y. Yamam. & Nann.-Bremek. to *Collosporopsis* (see the corresponding notes). Additionally, a replacement name is proposed for *Sta. reticulospora* Nann.-Bremek., R. Sharma & K.S. Thind, and this taxon is transferred to *Stemonitis* s.str. (see the corresponding notes).

For three other species, *Sta. irregularis* (Rex) Nann.-Bremek., R. Sharma & Y. Yamam., *Sta. mirabilis* (R.J. Benj. & Poitras) Nann.-Bremek., and *Sta. nannengae* (T.N. Lakh. & K.G. Mukerji) Nann.-Bremek., R. Sharma & Y. Yamam., this study proposes reverting to their basionyms within the morphologically broad and evidently polyphyletic *Comatricha* to avoid further taxonomic instability following the dissolution of *Stemonaria*: *Comatricha irregularis* Rex, *Comatricha mirabilis* R.K. Benj. & Poitras, and *Comatricha nannengae* T.N. Lakh. & K.G. Mukerji, respectively. According to the present data, *Com. irregularis* occupies a sister position to *L. cacographicum* and may potentially represent a distinct genus, although this requires further research beyond the scope of this study. *Comatricha mirabilis* displays banded-reticulate spores with high ridges, a morphology distinctly different from that of other reticulate-spored *Comatricha* species transferred here to *Stemonitopsis* (see below).

Finally, five species, *Sta. argentella*, *Sta. clausifila*, *Sta. laxa*, *Sta. laxiretis*, and *Sta. rufipes*, cannot be confidently assigned to another genus at present and have no other suitable synonyms. To clarify their taxonomic affinities, the holotypes of *Sta. argentella, Sta. clausifila*, and *Sta. laxiretis* were examined in detail for this study. The holotypes of *Sta. laxa* (TNS-M-Y-22047 = YY-360) and *Sta. rufipes* (TNS-M-Y-22051 = YY-1264) were not re-examined due to their poor condition: the specimen boxes contain very few sporocarps, and the material is heavily contaminated with fungi. Since the morphological data derived from these available materials do not conclusively support their transfer to other existing genera, retaining them within a genus from which the type species has been excluded creates a temporary nomenclatural anomaly. However, proposing provisional new combinations for these taxa into genera such as *Stemonitis* or *Comatricha* without solid phylogenetic justification would likely result in unnecessary names that will become obsolete. Similar pragmatic approaches have been utilized in previous myxomycete systematic studies to prioritize long-term taxonomic stability[14]. Therefore, these five species are temporarily retained under their current *Stemonaria* names pending future comprehensive studies.

***Stemonaria argentella* Y. Yamam., J. Jap. Bot. 65: 298 (1990), Fig. 9**

MycoBank number: MB126596.

Materials examined: NEPAL, Jumbesi, on plant litter in *Abies* forest, 10 Oct 1988, field, leg. Higuchi M. (holotype, TNS-M-Y-2450 = NE-88-77).

Notes: *Stemonaria argentella* was formally described from Nepal[90], and no new collections have been reported since. The key diagnostic characteristics of this species are its persistent, iridescent peridium (Fig. 9b–d) and the capillitium, which arises from the entire length of the columella and attaches to the remnants of the peridium (Fig. 9f, g, i). Through a detailed re-examination of the holotype (TNS-M-Y-2450 = NE-88-77; Fig. 9), it was discovered that the spore ornamentation is not spiculose as originally described, but consists of unevenly distributed, wart-like processes (Fig. 9k, l). New measurements of the holotype indicate sporocarps (0.8–)1.0–1.3(–1.5) mm in total height, (0.4–)0.5–0.6(–0.7) mm in diameter; stalk 0.3–0.5 mm long (30%–40% of the total height); spores (8.2–)8.6–9.1(–9.5) μm in diameter. This contrasts with the protologue[90], which reported sporocarps up to 1.7 mm in total height, 0.8 mm in diameter, with a stalk 1/5–3/5 of the total height, and spores 7.9–8.7 μm in diameter, with a light spot, bearing irregularly distributed warts. The holotype of this species was initially identified as a *Lamproderma* sp. (Fig. 9a) and was later described as *Sta. argentella*. Currently, *Sta. argentella* strongly corresponds to the typical characteristics of *Meriderma*[90], primarily due to its persistent peridium to which the capillitium is attached (Fig. 9b–d, f, i). However, all currently described species of *Meriderma* are nivicolous, whereas the holotype of *Sta. argentella* was collected in October in a high-altitude region of Nepal, which may not align with a strictly

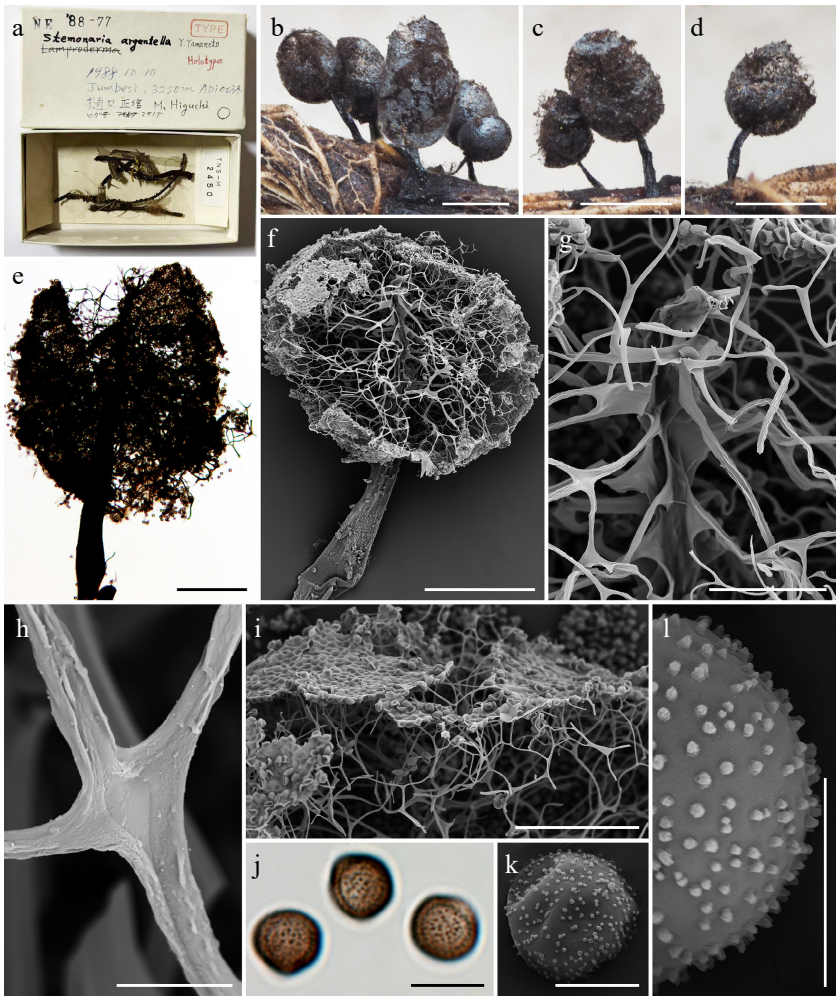

Fig. 9 Morphological characteristics of the holotype (TNS-M-Y-2450 = TNE-88-77) of *Stemonaria argentella*. (a) Herbarium labels and interior views of the herbarium box containing the holotype. (b)–(d) Mature sporocarps (DM). (e) Apical view of the sporotheca (LM). (f) Apical view of a sporotheca (SEM). (g) Apex of the columella (SEM). (h) Detail of the capillitium threads (SEM). (i) Connection between the capillitium and the peridium (SEM). (j) Spores (LM). (k) Spore (SEM). (l) Detail of the spore ornamentation (SEM). Scale bars: (b)–(d) = 1 mm; (e), (f) = 200 μm; (i) = 100 μm; (g) = 50 μm; (h), (j) = 10 μm; (k), (l) = 5 μm.

nivicolous ecology. The sporocarps could represent specimens that persisted after late snowmelt, given that the collection site is at high altitude. Attempts to obtain sequence data from the aged holotype (Fig. 9a) were unsuccessful, and no fresh material is available. Consequently, in the absence of phylogenetic data, it is not possible to revise *Sta. argentella* or determine its potential affinity with *Meriderma*.

***Stemonaria clausifila* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 98: 324 (1995), Fig. 10**

MycoBank number: MB414195.

Materials examined: JAPAN, Kochi Prefecture, Monobe-mura, Mt. Shiraga, on dead wood, 15 Aug 1991, field, leg. Yamamoto Y. (holotype, TNS-M-Y-22043 = YY-11745).

Notes: *Stemonaria clausifila* was described from Japan[91], and is known from only a few records in Japan[74]. Re-examination of the holotype (TNS-M-Y-22043 = YY-11745; Fig. 10) yielded new morphological data: sporocarps (2.2–)2.3–2.7(–2.9) mm in total height and 0.3–0.5 mm in diameter; stalk (0.2–)0.3–0.6(–0.9) mm long (15%–50% of the total height; Fig. 10b–d); surface net mesh (10–)24–44(–70) μm in diameter; spores (10.0–)11.0–11.7(–12.3) μm in diameter. These measurements largely match the protologue (sporocarps 2–2.5 mm in total height and 0.4–0.5 mm in diameter; stalk about 1/4 of the total height, and spores 9–11 μm in diameter, uniformly minutely spinulose). The columella displays greater complexity than previously reported: in addition to the form that dissipates at the sporotheca apex[91], a second form extends directly to the apex and branches to form the capillitium (Fig. 10e, j, k). SEM reveals that the spore ornamentation is distinctly long-spinose, lacking secondary ornamentation (Fig. 10m, o), rather than 'densely and minutely warted' as described in the protologue. The surface net is variably developed, often incomplete on the upper sporotheca but well-formed on the middle and lower parts, with irregularly polygonal to circular meshes (Fig. 10f–i). This contrasts with the protologue, which noted only a few meshes (but not a net)[91]. Due to the age of the holotype and its degraded state, DNA extraction and sequencing were unsuccessful, and no fresh material is available. Consequently, the phylogenetic placement of *Sta. clausifila* remains unavailable.

***Stemonaria laxiretis* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 93: 277 (1990), Fig. 11**

MycoBank number: MB12788.

Materials examined: JAPAN, Tokushima Prefecture, Kawashima-cho, Jingo, on dead wood, 29 Jun 1988, field, leg. Yamamoto Y. (holotype, TNS-M-Y-22048 = YY-6632).

https://doi.org/10.48130/mycosphere-0026-0012

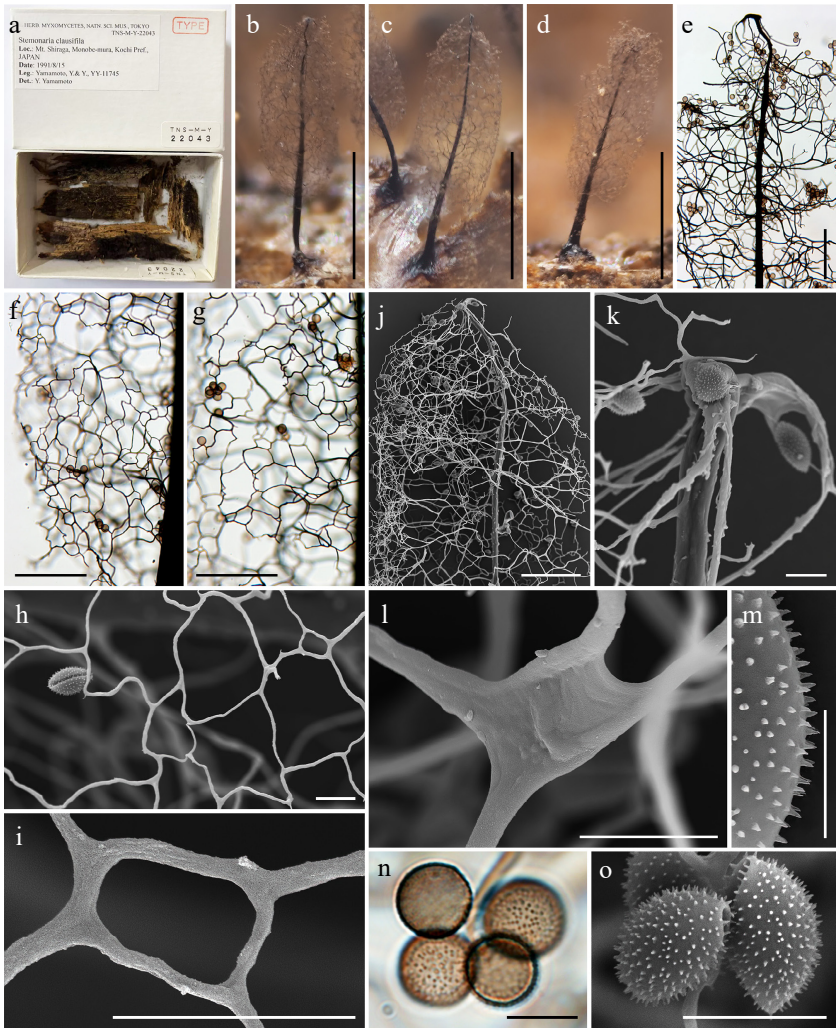

Fig. 10 Morphological characteristics of the holotype (TNS-M-Y-22043 = YY-11745) of *Stemonaria clausifila*. (a) Herbarium labels and interior views of the herbarium box containing the holotype. (b)–(d) Mature sporocarps (DM). (e) Apical view of the sporotheca (LM). (f), (g) Surface net (LM). (h), (i) Detail of the surface net (SEM). (j) Apical view of the sporotheca (SEM). (k) Apical view of the columella (SEM). (l) Detail of the capillitium threads (SEM). (m) Detail of the spore ornamentation (SEM). (n) Spores (LM). (o) Spores (SEM). Scale bars: (b)–(d) = 1 mm; (e)–(g), (j) = 100 μm; (h), (i), (k), (l), (n), (o) = 10 μm; (m) = 5 μm.

Notes: *Stemonaria laxiretis* was described from Japan[84]. The species displays the following morphological characteristics: a slender, loose capillitium that appears white under the dissecting microscope after spore dispersal (Fig. 11c, d). A detailed re-examination of the holotype (TNS-M-Y-22048 = YY-6632; Fig. 11) provides new morphological insights. New measurements of the holotype are as follows: sporocarps (2.4–)2.7–3.4(–3.9) mm in total height, 0.2–0.4 mm in diameter; stalk length (0.3–)0.5–0.8(–1.1) mm (15%–40% of the total height); and spores (7.1–)7.6–8.2(–8.8) μm in diameter. These values are largely consistent with the original description[84], which reported sporocarps ca. 5 mm in total height, a stalk about 1/3 of the total height, and spores 7–9 μm in diameter. The columella exhibits a distinctive morphology within *Stemonaria*: it is clavate and slightly expanded at the sporotheca apex (Fig. 11e, f), differing from the original account which described it as 'attenuate upwards, attaining the apex of the sporangium'[84]. Furthermore, SEM observation reveals that the spore ornamentation consists of unevenly distributed bacula whose bases are interconnected by faint lines, forming a delicate reticulum (Fig. 11m–o). The capillitium threads are densely covered with warts (Fig. 11k, l).

Stemonaria laxiretis may be similar to *Com. irregularis* (≡ *Sta. irregularis*) in sharing a whitish capillitial fringe and comparable spore size[26,59,92]. However, *Com. irregularis* differs in its irregularly long-conical to ovoid sporotheca (vs slender-cylindrical in *Sta. laxiretis*), its much longer stalk (1/2 to 2 times the sporocarp height vs 15%–40% in *Sta. laxiretis*), and its spore ornamentation of evenly distributed bacula of variable width, lacking the interconnecting lines and reticulum (see Eliasson et al.[26]: figs 17–29; Moreno et al.[59]: fig. 7) seen in *Sta. laxiretis* (Fig. 11m–o).

Unfortunately, due to the early collection date of the holotype and its prolonged preservation, the DNA has severely degraded, preventing successful sequencing. The lack of fresh material further compounds this issue. Consequently, molecular data remain unavailable to determine the phylogenetic placement of *Sta. laxiretis*.

• *Stemonitis* Gled., Methodus fungorum exhibens genera, species et varietates cum characters, differentia specifica, synonomis, solo, loco et observationibus: 140 (1753), sensu stricto

MycoBank number: MB12235.

Type: *Stemonitis fusca* Roth, Mag. Bot. 1 (2): 26 (1787).

Emended diagnosis: Stalked or short-stalked sporocarps or pseudoaethalia formed by crowded sporocarps. Peridium evanescent or persists as small flakes, free or attached to capillitium. Columella

extends nearly to the apex. Capillitium arising evenly along the entire length of the columella, branched and anastomosed. Spores brown to dark brown in mass, with uniformly thickened walls and warted-reticulate ornamentation. Under SEM, the reticulum formed by the walls is perforated in the lower part, resembling arched bridges or a Roman aqueduct, a comparison borrowed from Moreno et al.[78].

Accepted species: *Stemonitis amaurochaetoides* (Nann.-Bremek.) Shchepin, Gmoshinskiy, Schnittler & Novozh., *Ste. amphorocolumella* A. Vlasenko, G. Moreno & V. Vlasenko, *Ste. castillensis* T. Macbr., *Ste. conferta* W. L. Song & Shuang L. Chen, *Ste. curvicornis* W.L. Song & Shuang L. Chen, *Ste. emotoi* Nann.-Bremek. & Y. Yamam., *Ste. foliicola* Ing, *Ste. fusca* Roth, *Ste. fuscoides* (Nann.-Bremek. & Y. Yamam.) Shchepin, Prikhodko, Gmoshinskiy, Schnittler & Novozh., *Ste. gracilis* (Nann.-Bremek. & Y. Yamam.) Shchepin, Prikhodko, Gmoshinskiy, Schnittler & Novozh., *Ste. imperfecta* W.L. Song, M.L. Cai & Shuang L. Chen, *Ste. longa* (Peck) Massee, *Ste. palustris* W.L. Song, Bortnikov, Shuang L. Chen & Novozh., *Ste. pilosa* (Nann.-Bremek.) Bortnikov, W.L. Song, Gmoshinskiy, Shuang L. Chen & Novozh., *Ste. pinicola* Shchepin, Prikhodko, Gmoshinskiy, Schnittler & Novozh., *Ste. pinnatiapicalis* W.L. Song, Gmoshinskiy, Bortnikov, Novozh. & Shuang L. Chen, *Ste. rispaudii* (Hagelst.) Shchepin, Bortnikov, S.L. Stephenson, Schnittler & Novozh., and *Ste. spinimuralis* W.L. Song & Shuang L. Chen.

Morphospecies included in the genus but not yet phylogenetically studied: *Ste. curiosa* (Nann.-Bremek. & Y. Yamam.) W.L. Song, Bortnikov, Novozh. & Shuang L. Chen, *Ste. liaoningensis* (B. Zhang & Yu Li) Bortnikov, W.L. Song & Novozh., *Ste. longoides* Bortnikov, Novozh., Gmoshinskiy & W.L. Song, *Ste. marjana* Y. Yamam., *Ste. minuta* (Nann.-Bremek. & Y. Yamam.) W.L. Song, Bortnikov, Novozh. & Shuang L. Chen, *Ste. pseudonigra* (G. Moreno, W.C. Rosing, D.W. Mitch. & S.L. Stephenson) Bortnikov & W.L. Song, *Ste. reticulospora* (Ing & P.C. Holland) Bortnikov, W.L. Song, Novozh. & Shuang L. Chen, *Ste. rossii* Ejale, and *Ste. virginiensis* Rex.

Temporarily formally recognized species: *Ste. ellipsoidii* Ejale, *Ste. farrensis* T.N. Lakh. & K.G. Mukerji, *Ste. graciliformis* Nann.-Bremek., K.G. Mukerji & Pasricha, *Ste. inconspicua* Nann.-Bremek., *Ste. mussooriensis* G.W. Martin, K.S. Thind & Sohi, and *Ste. uvifera* T. Macbr.

Notes: Currently, 24 species are accepted within *Stemonitis*[6]. Recent phylogenetic studies have led to the transfer of several species from related genera into *Stemonitis*[88], including *Ste. amaurochaetoides* (≡ *Sym. amaurochaetoides* Nann.-Bremek.), *Ste. fuscoides* (≡ *Sta. fuscoides*), *Ste. gracilis* (≡ *Sta. gracilis*), *Ste. longa* (≡ *Sta. longa*), and *Ste. pinicola* (≡ *Stemonitopsis amoena* (Nann.-Bremek.) Nann.-Bremek.). Phylogenetic analysis conducted in this study (Fig. 1) supports a redefined, monophyletic concept of *Stemonitis* s.str., a clade unified by a warted-reticulate spore

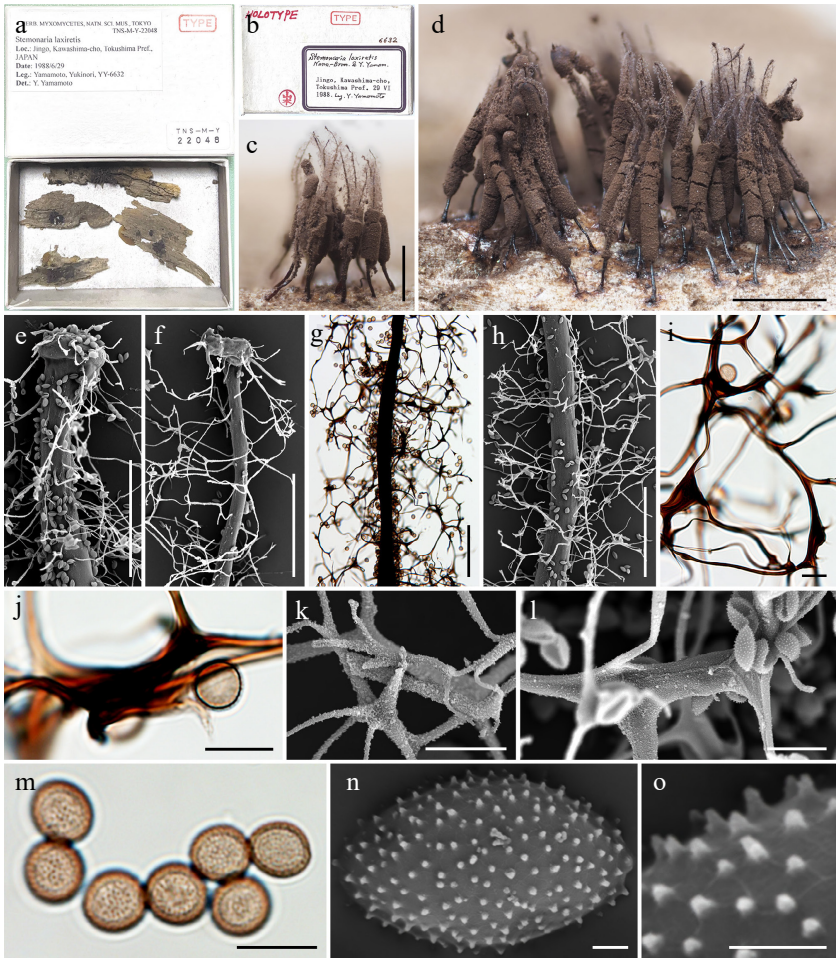

Fig. 11 Morphological characteristics of the holotype (TNS-M-Y-22048 = YY-6632) of *Stemonaria laxiretis*. (a) Herbarium labels and interior views of the herbarium box containing the holotype. (b) Herbarium labels of the herbarium box containing the holotype. (c), (d) Mature sporocarps (DM). (e), (f) Apical view of the columella (SEM). (g) Capillitium in the middle part of the sporotheca (LM). (h) Capillitium in the middle part of the sporotheca (SEM). (i), (j) Detail of the capillitium threads (LM). (k), (l) Detail of the capillitium threads (SEM). (m) Spores (LM). (n) Spore (SEM). (o) Detail of the spore ornamentation (SEM). Scale bars: (c), (d) = 2 mm; (e)–(h) = 100 μm; (i)–(m) = 10 μm; (n), (o) = 1 μm.

ornamentation and containing the type species *Ste. fusca*. Within this clade, the reticulum shows subtle variations that may correlate with distinct subclades (see Discussion), whereas other morphological characteristics are more variable. Based on an examination of type specimens or high-quality published images, five additional species possessing the warted-reticulate spore type are transferred to *Stemonitis* s.str., including *Stemonitopsis curiosa* Nann.-Bremek. & Y. Yamam., *Sta. liaoningensis*[93], *Sta. minuta*, *Comatricha pseudonigra* G. Moreno, W.C. Rosing, D.W. Mitch. & S.L. Stephenson[78], and *Comatricha reticulospora* Ing & P.C. Holland[94]. For *Sta. reticulospora* Nann.-Bremek., R. Sharma & K.S. Thind[24], a replacement name is proposed. The phylogenetic positions of these species will require future validation.

Species originally placed in *Stemonitis* but lacking the diagnostic warted-reticulate ornamentation are transferred to other genera where the evidence supports it. Taxa whose spores bear bacula with characteristically thickened apices are transferred to *Corallosporopsis*; these include *Ste. capillitionodosa*, *Ste. flavogenita*, *Ste. herbatica*, *Ste. laxifila*, *Ste. mediterraneensis*, *Ste. pallida*, and *Sta. pallidofila*. Species whose spores bear bacula or warts typically overlaid by a secondary ornamentation are transferred to *Symphytocarpus*; these include *Ste. ferruginea* (= *Ste. axifera* (Bull.) T. Macbr.), *Stemonitis plana* B. Zhang & Yu Li, *Stemonitis pseudoflavogenita* A. Vlasenko & Novozh., *Stemonitis rhizoideipes* Nann.-Bremek., R. Sharma & K.S. Thind, *Stemonitis sichuanensis* B. Zhang & Yu Li, and *Stemonitis splendens* Rostaf. Detailed notes for these species are provided in their respective sections.

Several species are retained in *Stemonitis* pending further study due to insufficient data. This includes *Ste. ellipsoidii*, *Ste. farrensis*, and *Ste. graciliformis*, for which SEM images of the types are unavailable. Material identified as *Ste. mussooriensis* from Mexico shows bacula with thickened apices, suggesting an affinity with *Corallosporopsis* (see Lizárraga et al.[95]: figs 27–31), but the complex taxonomic history of this name necessitates study of the type. The isotype of *Ste. uvifera* also displays bacula with potentially thickened apices (see Moreno et al.[71]: fig. 10), aligning it more closely with *Corallosporopsis*.

A notable case is *Ste. inconspicua*. Examination of a paratype indicates its spores have a large-meshed reticulum with seemingly imperforate walls (see Moreno et al.[71]: fig. 7), resembling some species of *Valtocarpus*[19]. However, its habitat differs from that typical of *Valtocarpus*, and the available SEM resolution is insufficient to conclusively confirm the absence of perforations. Therefore, this study refrains from transferring it to *Valtocarpus* at this time.

***Stemonitis amaurochaetoides* (Nann.-Bremek.) Shchepin, Gmoshinskiy, Schnittler & Novozh.**

MycoBank number: MB860492.

Synonym: *Symphytocarpus amaurochaetoides* Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C 70 (2): 220 (1967).

Materials examined: BELARUS, Brest Region, Pruzhany District, Belovezhskaya Pushcha National Park, vicinity of Hvoynik village, 52.7052° N, 23.9807° E, on rotten wood, 20 Sep 2021, field, leg. Moroz E.L. (MSK-F 43586-1). **RUSSIA**, Krasnoyarsk Territory, Beryozovsky District, Stolby National Park, on dead *Fomes fomentarius*, 2 Aug 2004, field, leg. Kosheleva A.P. (LE229354); Republic of Altai, Turochaksky District, vicinity of Yaylyu village, 51.7703° N, 87.6133° E, on decayed wood of *Betula pendula*, 17 Aug 2008, field, leg. Novozhilov Yu.K. and Schnittler M. (LE255019); Moscow Region, Odintsovo Urban District, vicinity of Skadovsky Zvenigorod Biological Station, 55.6992° N, 36.7297° E, on decayed wood of *Betula pendula*, 2 Aug 2017, field, leg. Zemlyanskaya I.V. and Novozhilov Yu.K. (LE278455); Republic of Tatarstan, Kazan city, surroundings of the 'Deep Lake' camp site, 55.8461° N, 48.9744° E, on decayed log of *Betula pendula*, 25 Aug 2016, field, leg. Zemlyanskaya I.V. (LE280022); Kamchatka Territory, Milkovsky District, vicinity of Lazo village, 55.4622° N, 159.7916° E, on decayed log of *Picea ajanensis*, 24 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325841); Tula Region, Shchyokinsky District, NW from Orlovo village, 53.9762° N, 37.1637° E, on bark of dead deciduous tree, 8 Jun 2014, field, leg. Gmoshinskiy V.I. and Matveev A.V. (MYX 7126); Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.8867° N, 37.6351° E, on rotten bark, 12 Sep 2024, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 24761); Moscow, Mytishi Urban District, Khlebnikovsky Forest Park, 55.9296° N, 37.5695° E, on polyporoid fungus (*Phellinus* sp.), 15 Jul 2023, field, leg. Gmoshinskiy V.I. and Ishenko Y.S. (MYX 25025).

Notes: *Stemonitis amaurochaetoides* was recently transferred to *Stemonitis* s.str. from *Symphytocarpus* by Shchepin et al.[88]. The isotype of *Ste. amaurochaetoides* was previously studied by Moreno et al.[71]. It is characterized by the formation of pseudoaethalia, dark brown spore mass, and spores ornamented with a simple reticulate pattern of perforated muri; the pillars do not exceed the tops of the muri, the perforations are sometimes inconspicuous, and the meshes are dense, numbering about 6–8 across the spore diameter (see Moreno et al.[71]: fig. 13e–g).

***Stemonitis amphorocolumella* Vlasenko, G. Moreno & V.A. Vlasenko, Phytotaxa 592 (1): 61 (2023)**

MycoBank number: MB829603.

Notes: *Stemonitis amphorocolumella* was described from dead wood of deciduous trees in the Republic of Altai, Russia[96]. The species is characterized by medium-sized sporocarps measuring 6–9 mm in total height, with a peridial remnant forming a membranous collar at the sporotheca base; the columella is amphora- or bottle-shaped at the apex; and spores are brown in mass, 9–11 μm in diameter, and finely reticulate[96]. To the best of current knowledge, the species has not been reported elsewhere. The SEM image provided in the protologue shows that the spore ornamentation consists of a fine-meshed reticulum with low, perforated muri that do not protrude beyond the mesh edges, consistent with a simple reticulate type.

***Stemonitis castillensis* T. Macbr., Bull. Lab. Nat. Hist. Iowa 2: 381 (1893), Fig. 12**

MycoBank number: MB146056.

Materials examined: BRAZIL, Pernambuco, Igarassu, Charles Darwin Ecological Refuge, 7.8130° S, 34.9536° W, on decayed wood, 17 Sep 2011, field, leg. Novozhilov Yu.K. (LE286562, LE286564).

Description: Sporocarps erect, stalked, densely gregarious, (13.6–)14.1–14.7(–15.3) mm in total height. Sporotheca cylindrical to tapering upwards, apex bluntly rounded, strong brown to moderate brown, 0.3–0.4 mm wide. Stalk black, shiny, (4.8–)5.2–5.4(–5.6) mm long, comprising 30%–40% of the total height, base forming an inconspicuous short cone. Hypothallus membranous, dark brown to deep brown, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex, unbranched, sinuous or filamentous at the apex. Capillitium arising perpendicularly from the entire length of the columella, lax to dense, deep brown to strong brown, with a large triangular expansion at the point of origin; branching complex, with membranous expansions frequent at the branching points, sometimes forming lines nearly parallel to the columella; threads nearly smooth, connecting to the surface net. Surface net well-developed, often incomplete at the sporotheca apex but complete elsewhere; meshes dense, irregularly polygonal to circular, of unequal diameter,

(6–)12–17(–37) μm; threads ornamented with irregularly distributed small warts, bearing spines of variable length. Spore concolorous with the sporotheca in mass, strong brown to deep orange in transmitted light, globose to subglobose, (6.9–)7.6–8.4(–9.4) μm in diameter, ornamented with a simple reticulate type with perforated muri, characterized by long pillars not exceeding the tops of the muri, sparse and unequal meshes, and prominent perforations, meshes numbering about 7–10 across the spore diameter. Plasmodium not observed.

Notes: *Stemonitis castillensis* was described from Nicaragua (Central America)[89]. According to the protologue, it differs from *Stemonitis maxima* Schwein. (= *Ste. fusca*) by its larger sporocarps, reaching 15–18 mm in total height[89]. Additional characteristics noted include a stalk comprising about one-third of the total height, spores measuring 7–8 μm in diameter, and conspicuous expansions in the internal network of the capillitium. In a monograph published the following year, Lister[97] stated without substantial argument that he recognized no characteristics distinguishing *Ste. castillensis* from *Ste. fusca* var. *rufescens* Lister, a variety he described in the same work.

In this study, two Brazilian (South American) specimens (LE286564 and LE286562) previously identified as *Ste. fusca* were examined in detail. These specimens correspond closely to the protologue of *Ste. castillensis*[89]: sporocarps attain 9.9–15.2 mm in total height (and may occasionally exceed this range; Fig. 12a, b), stalk represents about 39% of the total height (Fig. 12a, b), and spores (6.9–)7.6–8.4(–9.4) μm in diameter (compared to 7–8 μm in the protologue). Moreover, the internal capillitium net is lax to dense, sometimes forming lines nearly parallel to the columella, and also displays highly noticeable expansions (Fig. 12e, f). Considering these morphological agreements, together with the geographical provenance, this material is regarded as referable to *Ste. castillensis*. Given the phylogenetic distinction from *Ste. fusca* revealed in this study (Fig. 1), this study proposes the reinstatement of *Ste. castillensis* as a species separate from *Ste. fusca*.

***Stemonitis conferta* W. L. Song & Shuang L. Chen, sp. nov. Fig. 13**

MycoBank number: MB863118.

Etymology: *conferta* (Latin) crowded, dense, closely packed; from *confertus* (to pack together, to cram), referring to the very dense,

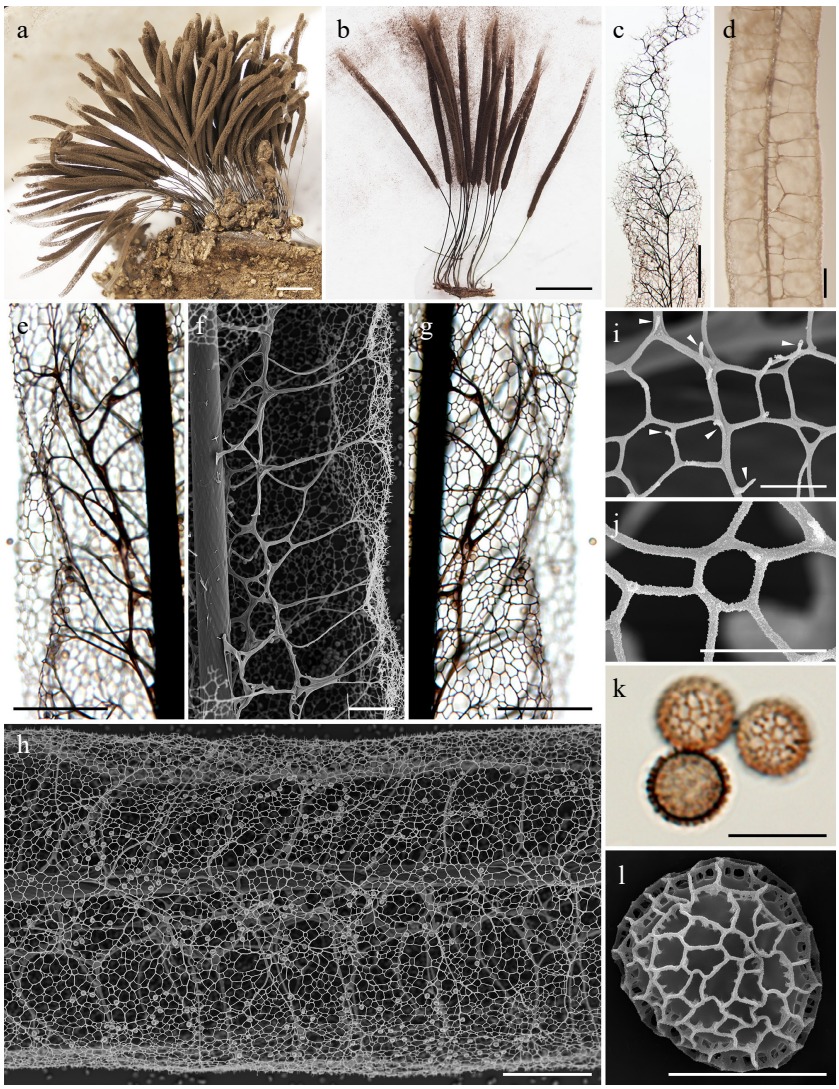

Fig. 12 Morphological characteristics of *Stemonitis castillensis* (a), (d), (j), (l) LE286562; (b), (c), (e)–(i), (k) LE286564. (a), (b) Mature sporocarps (DM). (c) Apical view of the sporotheca (LM). (d), (e) Capillitium in the middle part of the sporotheca (LM). (f) Capillitium in the middle part of the sporotheca (SEM). (g) Surface net (LM). (h) Surface net (SEM). (i) Spines on the surface net (SEM, arrows). (j) Detail of the surface net (SEM). (k) Spores (LM). (l) Spore (SEM). Scale bars: (a), (b) = 2 mm; (c) = 200 μm; (d), (e), (g), (h) = 100 μm; (f) = 50 μm; (i)–(k) = 10 μm; (l) = 5 μm.

compact growth of the sporocarps, which are so closely clustered that they can form a nearly continuous, mound-like pseudoaethalium.

Holotype: CHINA, Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, on rotten wood, 20 Jul 2024, field, leg. Song W.L., Meng Q., and Chen L.X. (HFNNU 10867, GenBank *nrSSU*: PX940064; *EF-1α*: PX961577; *mtSSU*: PX940081).

Diagnosis: Sporocarps in pseudoaethalium clusters, up to 1.5 mm in total height; stalk very short or absent; spores (7.7–)8.2–8.7(–9.8) μm in diameter, ornamented with a reticulum formed by muri and muri perforate, with 7–12 more or less equal-sized meshes across diameter.

Description: Sporocarps erect, sessile to short-stalked, densely gregarious, forming a pseudoaethalium, (0.8–)0.9–1.4 mm in total height. Sporotheca cylindrical to subglobose or slightly irregular, 0.4–0.5 mm wide, nearly equal in diameter throughout, apex bluntly rounded, dark brown. Stalk almost invisible under a stereomicroscope, extremely short and visible in transmitted light, black, opaque. Hypothallus membranous, dark brown to strong brown to deep orange, translucent, common to the colony. Peridium evanescent. Columella regular, black, tapering upwards, reaching the sporotheca apex, unbranched. Capillitium arising from the entire length of the columella, dense, sinuous, dark brown to pale brown, much and intricately branched; branching points often with membranous expansions; strong brown to deep orange; threads nearly smooth, ending at the sporotheca margin as spines. Surface net absent. Spore concolorous with the sporotheca in mass, dark reddish-orange to brown in transmitted light, globose to subglobose, (7.7–)8.2–8.7(–9.8) μm in diameter, ornamented with a reticulum formed by muri and muri perforate, meshes dense, numbering about 7–12 across the diameter. Plasmodium not observed.

Additional materials examined: CHINA, Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, on rotten wood, 17 Jul 2024, field, leg. Song W.L., Men Q., and Chen Y.J. (HFNNU 10868).

Distribution: currently known from Eastern China.

Habitat: on rotten wood.

Notes: *Stemonitis conferta* is characterized by small, dark grayish-brown to dark brown heaped sporocarps, forming a pseudoaethalium (Fig. 13a, b), with only (0.8–)0.9–1.4 mm in total height; stalk absent or, when present, visible only in transmitted light (Fig. 13c); spore ornamentation consisting of a reticulum formed by muri and muri perforate, with 7–12 more or less equal-sized meshes across the diameter (Fig. 13f–i). These characteristics make *Ste. conferta* somewhat similar to *Ste. amaurochaetoides*. However, *Ste. amaurochaetoides* has larger sporocarps (up to 5 mm in total height), lacks a stalk, possesses a columella that is absent or irregular when present, and its spores have 8–9 meshes across the diameter[19,71]. These differences distinguish *Ste. conferta* from *Ste. amaurochaetoides*. Phylogenetic analysis confirms that *Ste. conferta* belongs firmly within the *Stemonitis* s.str. clade, where it is closely related to *Ste. amphorocolumella, Ste. castillensis* and *Ste*. cf. *pilosa* (UBS/PP/TBE = 100/100/100; Fig. 1). This placement aligns with its simple reticulate spore ornamentation, which is consistent with the emended definition of *Stemonitis* s.str.

Stemonitis rispaudii, recently transferred to *Stemonitis* s.str. from *Paradiachea rispaudii* (Hagelst.) R.J.G. Hertel ex H. Neubert by Shchepin et al.[88], may also be related. It shares a similar habit of small, sessile, densely gregarious sporocarps, and a simple reticulate spore ornamentation formed by muri and muri perforate[98]. However, it differs in its much smaller perforations (the muri appear almost fused into ridges), persistent iridescent peridium at the sporotheca base, and larger spores ([8.6–]9.0–9.7[–10.3] μm in diameter).

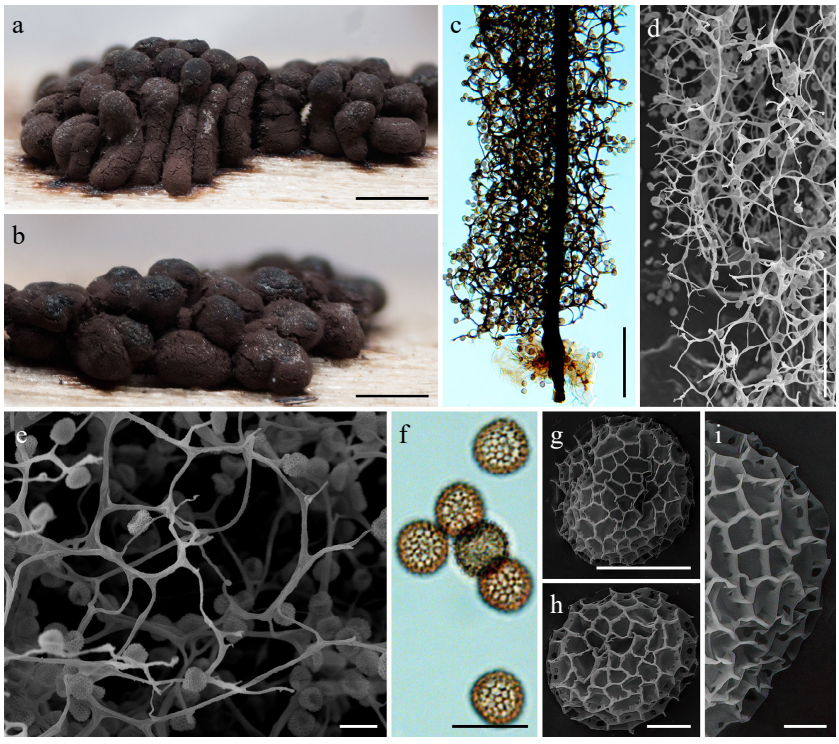

Fig. 13 Morphological characteristics of *Stemonitis conferta* (HFNNU 10867). (a), (b) Mature sporocarps (DM). (c) Capillitium and stalk of the sporocarp (LM). (d), (e) Edge of the sporotheca (SEM). (f) Spores (LM). (g), (h) Spore (SEM). (i) Detail of the spore ornamentation (SEM). Scale bars: (a), (b) = 1 mm; (c)–(e) = 100 μm; (f) = 10 μm; (g) = 5 μm; (h) = 2 μm; (i) = 1 μm.

***Stemonitis curiosa* (Nann.-Bremek. & Y. Yamam.) W.L. Song, Bortnikov, Novozh. & Shuang L. Chen, comb. nov. Fig. 14**

MycoBank number: MB863325.

Basionym: *Stemonitopsis curiosa* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 86: 239 (1983).

Materials examined: JAPAN, Kochi Prefecture, Ikegawa-cho, Mt. Tsutsujo, on dead wood, 29 Jul 1979, field, leg. Yamamoto Y. (holotype, TNS-M-Y-22056 = YY-352).

Notes: *Stemonitopsis curiosa* was described from Japan[99]. Examination of the holotype (TNS-M-Y-22056 = YY-352; Fig. 14) yielded the following measurements: sporocarps (2.9–)3.2–4.0(–4.3) mm in total height, 0.3–0.4 mm in diameter; stalk (0.6–)0.9–1.1(–1.4) mm long (20%–33% of the total height; Fig. 14b, c); surface net meshes (5–)11–21(–40) μm diameter; and spore (6.1–)6.8–7.4(–8.0) μm in diameter. These largely match the protologue (sporocarp 5–6 mm in total height, ca. 0.4 mm in diameter; stalk about 1/3 or a little over 1/3 of the total height; surface net meshes ca. 10–40 μm diameter; and spores 6–7 μm diameter). SEM reveals the spore ornamentation to be of the simple reticulate type with perforated muri, with low pillars not exceeding the muri tops and variably sized meshes (Fig. 14m). This ornamentation aligns with the circumscription of *Stemonitis* s.str., justifying the transfer to *Stemonitis* as *Ste. curiosa*.

The capillitium of *Ste. curiosa* is dense and intricately branched (Fig. 14h, i), contrasting with the original account of 'only slightly dichotomously branched'[99]. The branching nodes, however, are rounded and not membranously enlarged (Fig. 14j) as described. The surface net threads are nearly smooth (Fig. 14g), a potentially diagnostic characteristic. Unfortunately, due to the age of the holotype material, DNA sequencing was unsuccessful; thus, the phylogenetic position of *Ste. curiosa* remains unresolved.

***Stemonitis curvicornis* W.L. Song & Shuang L. Chen, sp. nov. Fig. 15**

MycoBank number: MB863119.

Etymology: *curvicornis* (Latin) with a curved horn, from *curvus* (curved, bent) and *cornu* (horn), referring to the frequently curved, wave-like shape of the columella as it extends to the apex of the sporotheca.

Holotype: CHINA, Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, 32.0873° N, 118.8411° E, on dead bark, 18 Jul 2024, field, leg. Song W.L., Meng Q., and Chen Y.J. (HFNNU 10969, GenBank *nrSSU*: PX940071; *EF-1α*: PX961592).

Diagnosis: Sporocarps measuring (2.6–)2.7–3.4(–3.5) mm in total height and 0.3–0.4 mm wide; stalk 0.6–0.8(–0.9) mm long (20%–33% of the total height); spores (7.6–)8.2–8.7(–9.1) μm in diameter, occasionally reaching up to 11.2 μm, ornamented with a simple reticulate type with perforated muri, pillars distinctly surpassing the muri tops, meshes numbering about 6–9 across the diameter.

Description: Sporocarps erect, stalked, densely gregarious in small groups, (2.6–)2.7–3.4(–3.5) mm in total height. Sporotheca elongate-cylindrical, tapering upwards, apex bluntly rounded, dark brown to deep brown to strong brown, 0.3–0.4 mm wide. Stalk black, shiny, 0.6–0.8(–0.9) mm long, 20%–33% of the total height, base conical. Hypothallus membranous, black to dark yellowish brown to translucent, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex and slightly sinuous. Capillitium arising nearly perpendicularly from

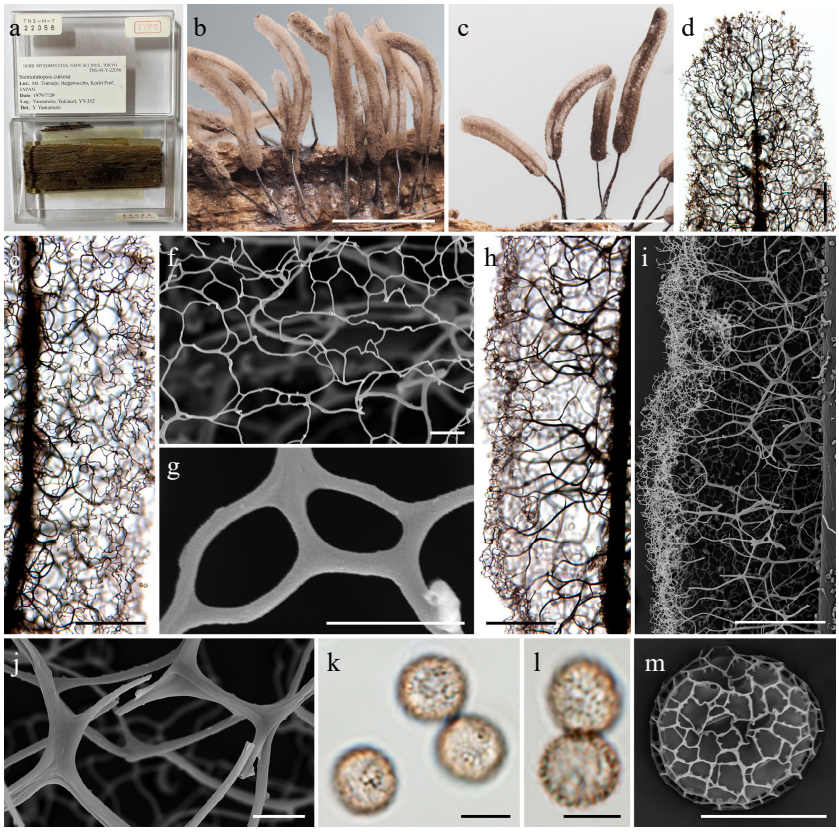

Fig. 14 Morphological characteristics of the holotype (TNS-M-Y-22056 = YY-352) of *Stemonitis curiosa* (≡ *Stemonitopsis curiosa*). (a) Herbarium labels and interior views of the herbarium box containing the holotype. (b), (c) Mature sporocarps (DM). (d) Apical view of the sporotheca (LM). (e) Surface net (LM). (f), (g) Detail of the surface net (SEM). (h) Capillitium in the middle part of the sporotheca (LM). (i) Capillitium in the middle part of the sporotheca (SEM). (j) Detail of the capillitium threads (SEM). (k), (l) Spores (LM). (m) Spore (SEM). Scale bars: (b), (c) = 2 mm; (d), (e), (h), (i) = 100 μm; (f), (j), (k) = 10 μm; (g), (k)–(m) = 5 μm.

the entire length of the columella, dense, deep brown to strong brown, much-branched; membranous expansions frequent at the branching points; threads nearly smooth, connecting to the surface net. Surface net well-developed, incomplete or nearly absent at the sporotheca apex but complete elsewhere; meshes irregularly polygonal to circular, of unequal diameter, (4–)8–14(–21) μm, threads sometimes sinuous, surface smooth. Spore concolorous with the sporotheca in mass, strong reddish-brown to moderate reddish-orange in transmitted light, globose to subglobose, (7.6–)8.2–8.7(–9.1) μm in diameter, rarely up to 11.2 μm (possibly malformed), with a clearly visible germination pore, bearing a simple reticulate type ornamentation with perforated muri, characterized by sparse and unequal meshes, numbering about 6–9 across the diameter, pillars distinctly surpassing the tops of the muri, and prominent perforations. Plasmodium not observed.

Additional materials examined: CHINA, Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, 32.0740° N, 118.8894° E, on dead bark, 11 Jul 2023, field, leg. Lin D., Song W.L., and Rao G. (HFNNU 10970, HFNNU 10971); Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, 32.0617° N, 118.8625° E, on dead bark, 30 Mar 2023, field, leg. Lin D., Song W.L., and Rao G. (HFNNU 10974).

Distribution: currently known from Eastern China.

Habitat: on dead bark.

Notes: Morphologically, *Ste. curvicornis* is most similar to *Ste. virginiensis*, as both may have a slightly sinuous columella at the sporotheca apex[100]. However, *Ste. virginiensis* has smaller spores (5–6.5 μm in the holotype; 5.6–8.2 μm in the syntype) with a broad reticulum of 3–5 meshes across the diameter[71,100]. *Stemonitis inconspicua* and *Ste. marjana* are also similar in having small sporocarps and reticulated spores, but the reticulum of *Ste. inconspicua* lacks perforations[71,101], and the spores of *Ste. marjana* are larger ([8.5–]9.1–10.2[–10.9] μm in diameter for holotype in this study; 8.8–9.8 μm in protologue), with pillars that do not surpass the muri tops (see below). The newly described *Ste. palustris* shares the curved columella at the sporotheca apex but is otherwise distinct (see Notes for *Ste. palustris*).

Phylogenetically, *Ste. curvicornis* forms a well-supported clade (UBS/PP/TBE = 100/100/100; Fig. 1) sister to a group containing *Ste. pinnatiapicalis* and *Ste.* aff. *fusca*. It can be distinguished from *Ste. pinnatiapicalis* by its slightly larger spores, smaller sporocarps, and less abundantly warted surface net threads. Compared to the much larger sporocarps of the examined specimens of *Ste.* aff. *fusca*, *Ste. curvicornis* is notably smaller and possesses a different columella termination (filamentous and branching in *Ste.* aff. *fusca*). Based on this suite of morphological distinctions and its unique phylogenetic position, *Ste. curvicornis* is described as a new species.

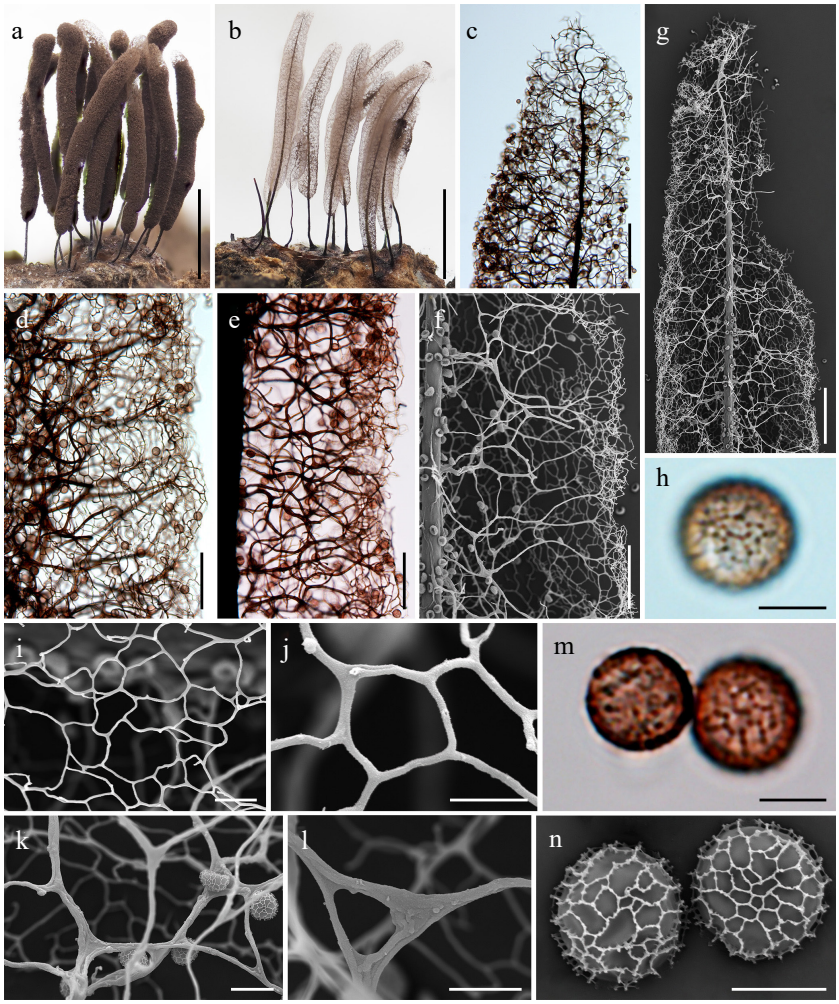

Fig. 15 Morphological characteristics of *Stemonitis curvicornis* (a)–(e), (h), (m) HFNNU 10970; (g), (f), (i)–(l), (n) HFNNU 10969. (a), (b) Mature sporocarps (DM). (c) Apical view of the sporotheca (LM). (d) Surface net (LM). (e) Capillitium in the middle part of the sporotheca (LM). (f) Capillitium in the middle part of the sporotheca (SEM). (g) Apical view of a sporotheca (SEM). (h) Spore (LM). (i), (j) Detail of the surface net (SEM). (k), (l) Detail of the capillitium threads (SEM). (m) Spores (LM). (n) Spore (SEM). Scale bars: (a), (b) = 2 mm; (c), (g) = 100 μm; (d)–(f) = 50 μm; (i), (k), (l) = 10 μm; (h), (j), (m), (n) = 5 μm.

***Stemonitis emotoi* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 87: 463 (1984), Figs 16, 17**

MycoBank number: MB107435.

Materials examined: JAPAN, Kochi Prefecture, Gohoku-son, Kamiyakawa, on a dead twig of *Morus*, 24 Aug 1980, field, leg. Yamamoto Y. (holotype, TNS-M-Y-22053 = YY-765). **CHINA**, Henan Province, Nanyang City, Baotianman National Nature Reserve, 33.5019° N, 111.9431° E, on dead bark, 23 Jun 2016, field, leg. Gao Y. and Wang G.W. (HFNNU 10801, HFNNU 10802); Anhui Province, Luan City, Tiantangzhai National Forest Park, 31.1574° N, 115.7922° E, on dead bark, 24 Oct 2015, field, leg. Gao Y. and Wang G.W. (HFNNU 12379); Henan Province, Xinyang City, Jingangtai National Geopark, 31.7429° N, 115.4939° E, on dead bark, 1 Sep 2022, field, leg. Lin D. and Song W.L. (HMAS 0287343).

Notes: *Stemonitis emotoi* was described from Japan[24] and was later demoted to the rank of a variety of another species as *Ste. mussooriensis* var. *emotoi* (Nann.-Bremek. & Y. Yamam.) Y. Yamam.[63]. In the protologue, its spores were described as '9–10 μm in diam., warted with dark warts, which are slightly swollen at the apex, and 0.5–0.8 μm tall, arranged in rows which form a small meshed reticulation, of about 7 meshed across the diameter'[24]. However, detailed re-examination of the holotype of *Ste. emotoi* (TNS-M-Y-22053 = YY-765) yielded different results. Measurements conducted in this study showed the spore diameter to be (10.2–)10.9–12.0(–12.5) μm. Furthermore, SEM observations in this study revealed that the actual spore ornamentation of the holotype corresponds to the simple reticulate type, characterized by distinct pillars extending beyond the tops of the muri and relatively conspicuous perforations (Fig. 16k, l).

In contrast, the spore ornamentation of *Ste. mussooriensis* has been described as consisting of abundant and prominent warts, 10.5–12.5 μm in diameter[63], which differs from the ornamentation type observed in the holotype of *Ste. emotoi*. Additionally, a Mexican specimen identified as *Ste. mussooriensis* (AH 31923) displays a spore morphology[95] distinct from that of the *Ste. emotoi* holotype, and may represent a different taxon possibly belonging to *Corallosporopsis*. Given these discrepancies and the inherent difficulty of accurately assessing spore ornamentation by light microscopy alone, it is considered premature to treat *Ste. emotoi* as a synonym or variety of *Ste. mussooriensis* without a re-examination of the latter's type material. Therefore, *Ste. emotoi* is reinstated as a distinct species.

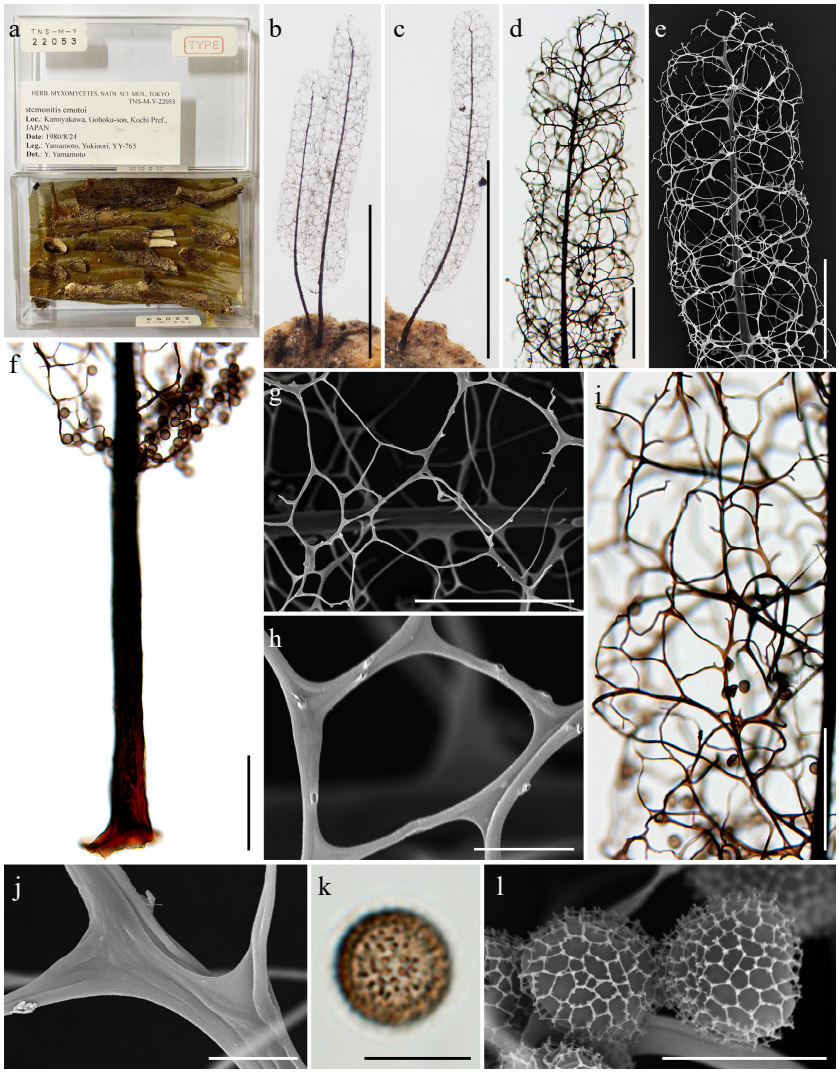

Fig. 16 Morphological characteristics of the holotype (TNS-M-Y-22053 = YY-765) of *Stemonitis emotoi*. (a) Herbarium label and interior views of the herbarium box containing the holotype. (b), (c) Mature sporocarps (DM). (d) Apical view of the sporotheca (LM). (e) Apical view of the sporotheca (SEM). (f) Stalk (LM). (g), (h) Detail of the surface net (SEM). (i) Capillitium and surface net in the middle part of the sporotheca (LM). (j) Detail of the capillitium threads (SEM). (k) Spore (LM). (l) Spores (SEM). Scale bars: (b), (c) = 2 mm; (d)–(f) = 200 μm; (g), (i) = 100 μm; (h), (j)–(l) = 10 μm.

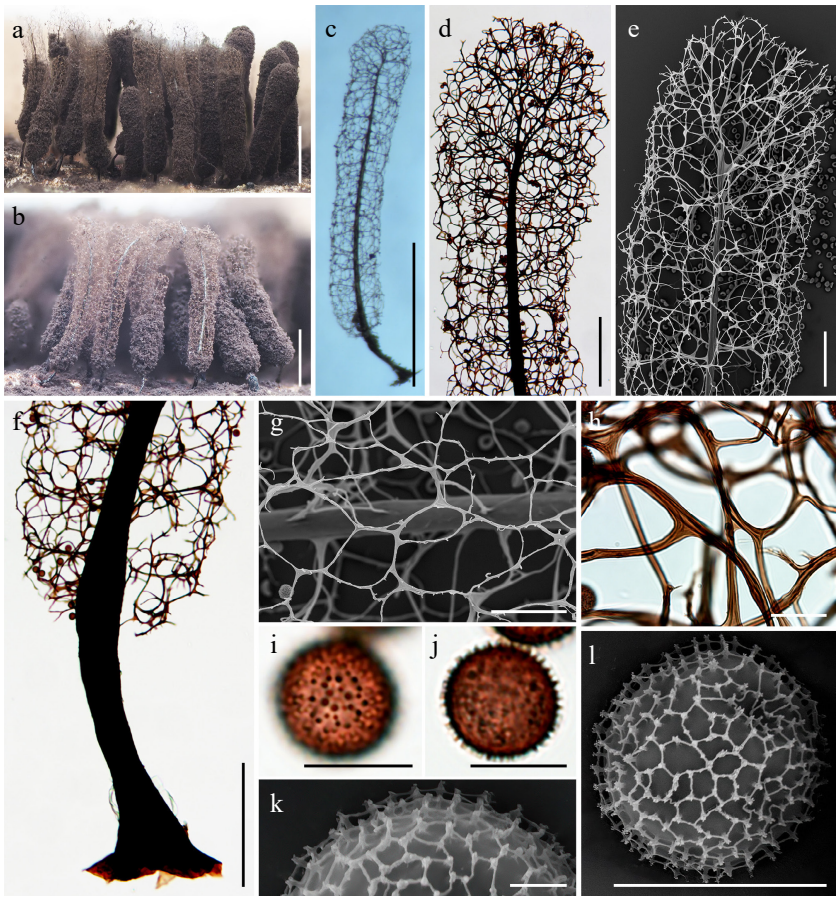

Fig. 17 Morphological characteristics of *Stemonitis emotoi* (a)–(d), (f), (h), (i), (j) HFNNU 10801; (e), (g), (k), (l) HFNNU 10802. (a)–(c) Mature sporocarps (DM). (d) Apical region of the sporocarp (LM). (e) Apical region of the sporocarp (SEM). (f) Stalk (LM). (g) Detail of the surface net (SEM). (h) Detail of the capillitium threads (LM). (i), (j) Spore (LM). (k) Detail of the spore ornamentation (SEM). (l) Spore (SEM). Scale bars: (a)–(c) = 1 mm; (d), (f) = 200 μm; (e) = 100 μm; (g) = 50 μm; (h) = 20 μm; (i), (j), (l) = 10 μm; (k) = 2 μm.

The four specimens examined in this study (HFNNU 10801, 10802, 12379; HMAS 0287343, Fig. 17) generally conform to the protologue[24] and to the revised understanding of the holotype (Fig. 16). The spore diameter of these newly examined specimens (including ornamentation) is (11.0–)11.7–12.6(–13.1) μm; although slightly larger than that of the holotype, their spore ornamentation is almost identical. Another minor variation is seen in the stalk proportion: the holotype has a relatively slender stalk (25%–33% of the total height, Fig. 16b, c, f), whereas the studied specimens have shorter stalks (14%–20% of the total height, Fig. 17a–c, f). No other significant morphological differences were observed. Due to the age of the holotype, DNA sequencing could not be obtained from it. However, phylogenetic analysis of the newly sequenced specimens in this study places *Ste. emotoi* in an independent, well-supported clade (UBS/PP/TBE = 100/100/100; Fig. 1), showing a close phylogenetic relationship to the newly described species *Ste. curvicornis*, *Ste. pinnatiapicalis*, and *Ste.* aff. *fusca* (UBS/PP/TBE = 100/100/100).

***Stemonitis foliicola* Ing, Trans. Brit. Mycol. Soc. 50(4):555 (1967)**

MycoBank number: MB339643.

Materials examined: BELARUS, Gomel Region, Svyetlahorsk District, Vydrica Nature Reserve, 52.7532° N, 29.7571° E, on rotten wood, 4 Aug 2021, field, leg. Moroz E.L. (MSK-F 43589); Grodno Region, Masty District, Lipichanskaya Pushcha Nature Reserve, vicinity of Shestily village, 53.4270° N, 24.8896° E, on rotten wood, 2 Nov 2021, field, leg. Moroz E.L. (MSK-F 43592); Vitebsk Region, Rasony District, vicinity of Milovidy village, 55.9340° N, 28.4249° E, on rotten wood, 13 May 2019, field, leg. Moroz E.L. (MSK-F 43602). **CHINA**, Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, on rotten wood, 18 Jul 2024, field, leg. Song W.L., Meng Q., and Chen Y.J. (HFNNU 10964); Hubei Province, Yichang City, Xingshan County, on dead twig, 27 Jun 2017, field, leg. Gao Y. (HFNNU 12189); Anhui Province, Luan City, Tiantangzhai National Forest Park, on dead twig, 26 Jul 2016, field, leg. Wang G.W. and Gao Y. (HFNNU 13264). **RUSSIA**, Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.9238° N, 158.7063° E, on decayed log of *Salix* sp., 14 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325205); Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.9319° N, 158.7255° E, on strongly decayed log of *Salix* sp., 15 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325258); Jewish Autonomous Region, Obluchensky District, Bastak Nature Reserve, 49.0882° N, 133.0834° E, on decayed deciduous wood, 27 Jun 2022, field, leg. Bortnikov F.M. (LE348878).

Notes: *Stemonitis foliicola* was described from England[102], and is considered geographically widespread[103–106]. The protologue, based on material from decaying oak leaves, is schematic and lacks images, making detailed comparisons difficult. Specimens examined in this study (HFNNU 10964, 12189, 13264; LE325205, 348878; MSK-F 43589, 43592, 43602) largely match the original description[102] in key characteristics, despite occurring on different substrates (likely representing ecological variation). Sporocarps measure (2.8–)3.4–4.8(–5.6) mm in total height (Fig. 18a, d), which is close to the protologue; capillitium relatively dense, with membra-

nous expansions at branching points sometimes appearing merely rounded (Fig. 18f, h–l), representing a slight deviation; surface net fragile and locally incomplete (Fig. 18g, m–o), meshes measuring (7–)12–18(–39) μm in diameter, essentially matching the described 10–15 μm; and spores (6.7–)7.8–8.7(–9.8) μm in diameter, consistent with the originally reported 7.5–8 μm. SEM reveals that the spores are ornamented with a simple reticulate type with perforated muri, forming uneven meshes, pillars that generally surpass (or sometimes equal) the muri tops, and conspicuous perforations (Fig. 18p–t); this provides more detail than the original note of 'closely reticulated with small spines with at least 20 meshes to the hemisphere'[102].

In the three-gene phylogenetic tree (Fig. 1), these specimens form a well-supported clade (UBS/PP/TBE = 99/-/94) with a previously reported *Ste. foliicola* sequence (voucher: AMFD505, GB number: MK041077)[27]. However, because the type specimen was unavailable for direct morphological comparison, particularly of the spore ornamentation, which is challenging to assess by light microscopy, and because most of the examined specimens were not collected from leaves, this study refrains from unequivocally identifying them as *Ste. foliicola*. A detailed re-examination of the type material and of specimen AMFD505 is required to confirm the application of the name.

***Stemonitis fusca* Roth, Mag. Bot. 1 (2): 26 (1787)**

MycoBank number: MB240909.

Materials examined: BELARUS, Brest Region, Pruzhany District, Belovezhskaya Pushcha National Park, vicinity of Hvoynik village, 52.6865° N, 23.9878° E, on rotten wood, 20 Sep 2021, field, leg. Moroz E.L. (MSK-F 40946); Grodno Region, Masty District, Lipichanskaya Pushcha Nature Reserve, vicinity of Shestily village, 53.4273° N, 24.8895° E, on bark, 25 May 2022, field, leg. Moroz E.L. (MSK-F 42887); Brest Region, Kamyenyets District, Belovezhskaya Pushcha National Park, vicinity of Kamenyuki village, 52.5984° N, 23.7845° E, on rotten wood, 6 Oct 2022, field, leg. Moroz E.L. (MSK-F 43008); Brest Region, Pruzhany District, Belovezhskaya Pushcha National Park, vicinity of Hvoynik village, 52.7079° N, 23.9861° E, on rotten wood, 22 Sep 2021, field, leg. Moroz E.L. (MSK-F 43582-1); Gomel Region, Loyew District, Dnepro-Sozhsky Nature Reserve, vicinity of Podrachitska village, 52.0218° N, 30.8044° E, on rotten wood, 19 Jun

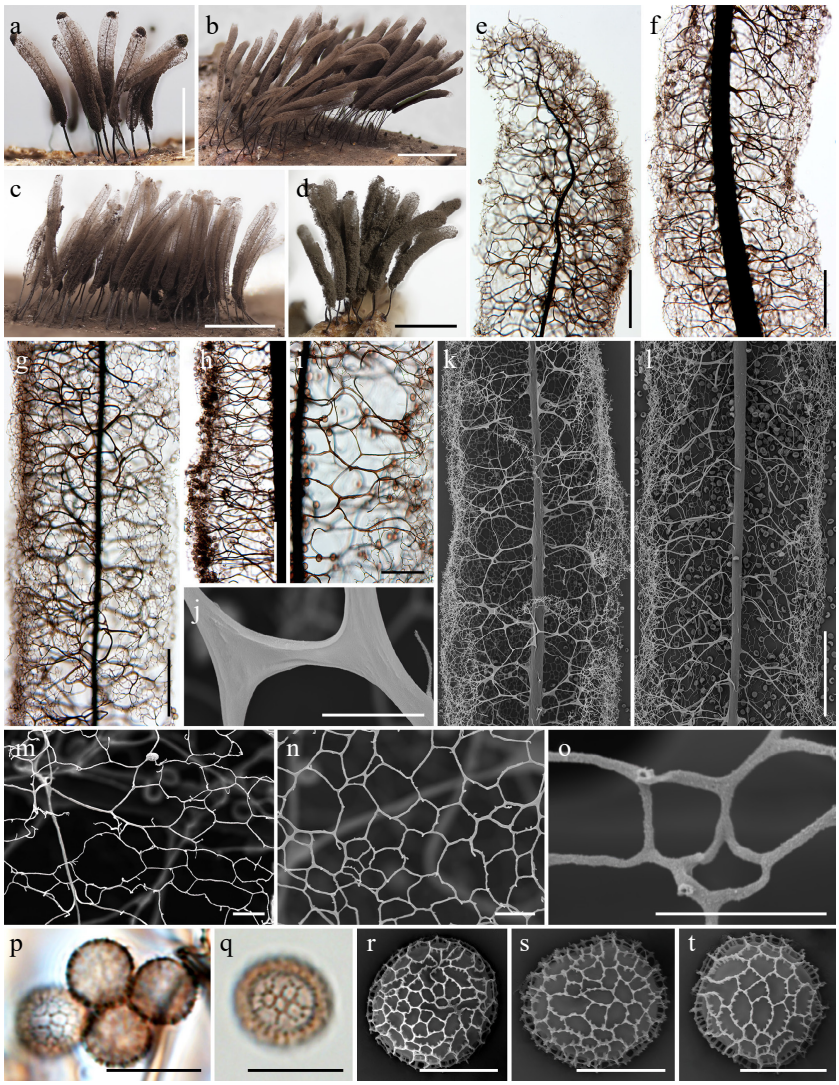

Fig. 18 Morphological characteristics of *Stemonitis* cf. *foliicola* (a), (i), (m), (r) HFNNU 10964; (b), (h) HFNNU 12189; (c), (n), (q), (p) MSK-F 43589; (d) LE348878; (e), (g), (l), (o), (s) HFNNU 13264; (f), (j), (k), (t) MSK-F 43592. (a)–(d) Mature sporocarps (DM). (e) Apical view of the sporotheca (LM). (f) Capillitium in the middle part of the sporotheca (LM). (g) Surface net (LM). (h), (i) Capillitium in the middle part of the sporotheca (LM). (j) Detail of the capillitium threads (SEM). (k), (l) Capillitium in the middle part of the sporotheca (SEM). (m)–(o) Detail of the surface net (SEM). (p), (q) Spores (LM). (r)–(t) Spore (SEM). Scale bars: (a)–(d) = 1 mm; (e)–(h), (k), (l) = 100 μm; (i) = 50 μm; (j), (m), (n), (p), (q) = 10 μm; (o), (r)–(t) = 5 μm.

2023, field, leg. Moroz E.L. (MSK-F 43584); Gomel Region, Svyetlahorsk District, Vydrica Nature Reserve, 52.7677° N, 29.8028° E, on rotten wood, 4 Aug 2021, field, leg. Moroz E.L. (MSK-F 43606). **CHINA**, Jiangxi Province, Yichun City, Mingyue Mountain National Forest Park, on rotten wood, 16 Jul 2022, field, leg. Chen S.L. and Yan S.Z. (HFNNU 4212); Shandong Province, Haiyang City, Zhaohu Mountain National Forest Park, 36.8694° N, 121.2349° E, on rotten wood, 13 Aug 2023, field, leg. Rao G. and Song W.L. (HFNNU 4466); Guangdong Province, Zhaoqing City, Dinghu Mountain National Nature Reserve, on rotten wood, 26 Nov 2024, field, leg. Song W.L. (HFNNU 12439); Guangxi Province, Nanning City, Daming Mountain National Nature Reserve, on rotten wood, 19 Dec 1997, field, leg. Chen S.L. (HMAS 72420); Anhui Province, Anqing City, Yaoluoping National Nature Reserve, 30.9868° N, 116.0891° E, on rotten wood, 21 Oct 2021, field, leg. Du Q. (HMAS 0295537). **RUSSIA**, Jewish Autonomous Region, Obluchensky District, Bastak Nature Reserve, 49.1256° N, 133.1327° E, on decayed deciduous wood, 28 Jun 2022, field, leg. Bortnikov F.M. (LE348891); Jewish Autonomous Region, Obluchensky District, Bastak Nature Reserve, 49.0947° N, 133.0602° E, on decayed wood of *Fraxinus* sp., 2 Jul 2022, field, leg. Bortnikov F.M. (LE348930); Volgograd Region, Sredneakhtubinsky District, vicinity of Kuropatka lake, 48.5883° N, 44.6589° E, on decayed log of *Populus nigra*, 26 Aug 2018, field, leg. Zemlyanskaya I.V. (LE279120); Moscow Region, Odintsovo Urban District, vicinity of Skadovsky Zvenigorod Biological Station, 55.7011° N, 36.8014° E, on decayed log of *Quercus robur*, 2 Aug 2017, field, leg. Zemlyanskaya I.V. (LE279571); Karachayevo-Circassian Republic, Karachayevsky District, Teberda Nature Reserve, 43.4180° N, 41.7241° E, on decayed wood of *Quercus robur*, 22 Aug 2012, field, leg. Erastova D.A. and Morozova Yu.A. (LE291133); Primorye Territory, Terneysky District, Sikhote-Alin Nature Reserve, 45.3154° N, 136.4754° E, on strongly decayed wood of *Pinus koraiensis*, 26 Aug 2014, field, leg. Novozhilov Yu.K., Schnittler M., Shchepin O.N., and Erastova D.A. (LE302352); Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.9214° N, 158.7158° E, on decayed log of *Salix udensis*, 11 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325066); Kamchatka Territory, Milkovsky District, vicinity of Lazo village, 55.4503° N, 159.7951° E, on strongly decayed log of *Alnus hirsuta*, 21 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325706); Kamchatka Territory, Yelizovsky District, slope of Avachinskaya volcano, 53.2299° N, 158.6775° E, on strongly decayed log of *Betula ermanii*, 28 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325855); Kamchatka Territory, Yelizovsky District, slope of Avachinskaya volcano, 53.2299° N, 158.6775° E, on strongly decayed log of *Alnus fruticosa*, 28 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325884); Primorye Territory, Khasansky District, Kedrovaya Pad Nature Reserve, 43.1667° N, 131.4990° E, on decayed deciduous wood, 18 Jul 2020, field, leg. Bortnikova N.A. (LE328015); Leningrad Region, Vyborgsky District, Bolshoy Beryozovy Island, 60.2651° N, 28.6756° E, on a log of *Betula pubescens*, 5 Sep 2024, field, leg. Novozhilov Yu.K. and Luptakova A.D. (LE346775); Amur Region, Zeysky District, Zeya Nature Reserve, 53.8803° N, 127.3322° E, on decayed wood, 17 Sep 2024, field, leg. Bortnikov F.M. and Bortnikova N.A. (LE353081); Karachayevo-Circassian Republic, Karachayevsky District, Teberda Nature Reserve, 43.4464° N, 41.7109° E, on decayed wood of *Sorbus* sp., 18 Aug 2012, field, leg. Novozhilov Yu.K., Erastova D.A. and Morozova Yu.A. (LE353263 previously erroneously published in GenBank as LE290927b); Krasnodar Territory, Anapsky District, Utrish Nature Reserve, Suchoy Liman lake, 44.7556° N, 37.4609° E, on bark of dead trees, 30 May 2017, field, leg. Gmoshinskiy V.I. and Gubanov E.S. (MYX 8685); Pskov Region, Loknyansky Municipal District, Polystovskiy State Nature Reserve, 57.0833° N, 30.5121° E, on the inner surface of rotten bark of a deciduous tree, 14 Jul 2021, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 17763); Vladimir Region, Sudogodsky District, vicinity of Lobanovo village, 56.0130° N, 40.8131° E, on rotten wood, 10 Nov 2021, field, leg. Mishulin A.A. and Gmoshinskiy V.I. (MYX 19459); Vladimir Region, Sudogodsky District, vicinity of Lobanovo village, 56.0090° N, 40.8130° E, on rotten wood, 10 Nov 2021, field, leg. Mishulin A.A. and Gmoshinskiy V.I. (MYX 19501).

Notes: *Stemonitis fusca* is a morphologically highly polymorphic species with a wide distribution and ecological range[13,17,100]. A primary issue concerning *Ste. fusca* is understanding what constitutes the 'true' *Ste. fusca*.

In the three-gene phylogenetic tree constructed in this study, specimens preliminarily identified as *Ste. fusca* are resolved into two distantly separate clades (Fig. 1). One clade comprises specimens such as LE348930, HFNNU 4466, MSK-F 43606, and MYX 17763. The other clade is represented by specimens such as LE302352, MSK-F 43582, HMAS 0295537, HFNNU 4212, and MYX 19501. These specimens exhibit morphological polymorphism; however, this range of morphological characteristics aligns closely with the modern conception of *Ste. fusca*. A detailed analysis of *Ste. fusca* was previously conducted by Castillo et al.[100], who also noted considerable variation in characteristics, including spore ornamentation observed under SEM. However, it should be noted that the neotype they selected (E&E 2697, USA) has spores in which the pillars do not exceed the height of the bridges (see Castillo et al.[100]: figs 41, 42). Therefore, the specimens from the first clade (LE348930 et al.) are identified as *Ste.* aff. *fusca*, since, despite their overall similarity, they have pillars that exceed the bridges (Fig. 19m, n). The specimens from the second clade, here designated as *Ste. fusca* agg., may in fact represent several closely related species (Fig. 20). However, this study refrains from conducting a detailed analysis of *Ste. fusca* at this time, as it is a widespread species that requires separate study. The choice of a neotype from American specimens, given that *Ste. fusca* was described from Germany, cannot be considered entirely successful. Nonetheless, it is acknowledged that the authentic *Ste. fusca* may have a broad geographical range.

***Stemonitis fuscoides* (Nann.-Bremek. & Y. Yamam.) Shchepin, Prikhodko, Gmoshinskiy, Schnittler & Novozh.**

MycoBank number: MB860494.

Synonym: *Stemonaria fuscoides* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 87: 460 (1984).

Notes: *Stemonitis fuscoides* was recently transferred to *Stemonitis* from *Stemonaria* by Shchepin et al.[88]. This species was recorded on dead wood of *Prunus* sp. in Japan[24]. The protologue reports medium-sized, brown sporocarps (4–5 mm in total height, ca. 0.5 mm in diameter) with a relatively dense capillitium that does not form a surface net; spores measure 8.5–9.5 μm in diameter and are ornamented with rows of dark spinules (ca. 0.5 μm height) that form a fine reticulum of about seven meshes across the diameter; no SEM images were provided. An attempt was made to examine the isotype (TNS-M-Y-22044 = YY-412) of this species, but the herbarium box no longer contained sporocarps (which were already absent during a check in 2005). Based on the study of specimen MYX 12516, Shchepin et al.[88] proposed the transfer of *Sta. fuscoides* to *Stemonitis* as *Ste. fuscoides*. An SEM image provided in that work (see Shchepin et al.[88]: fig. S27d) shows spores with a fine reticulate ornamentation of perforated muri, consistent with the circumscription of *Stemonitis* s.str.

***Stemonitis gracilis* (Nann.-Bremek. & Y. Yamam.) Shchepin, Prikhodko, Gmoshinskiy, Schnittler & Novozh. Fig. 21**

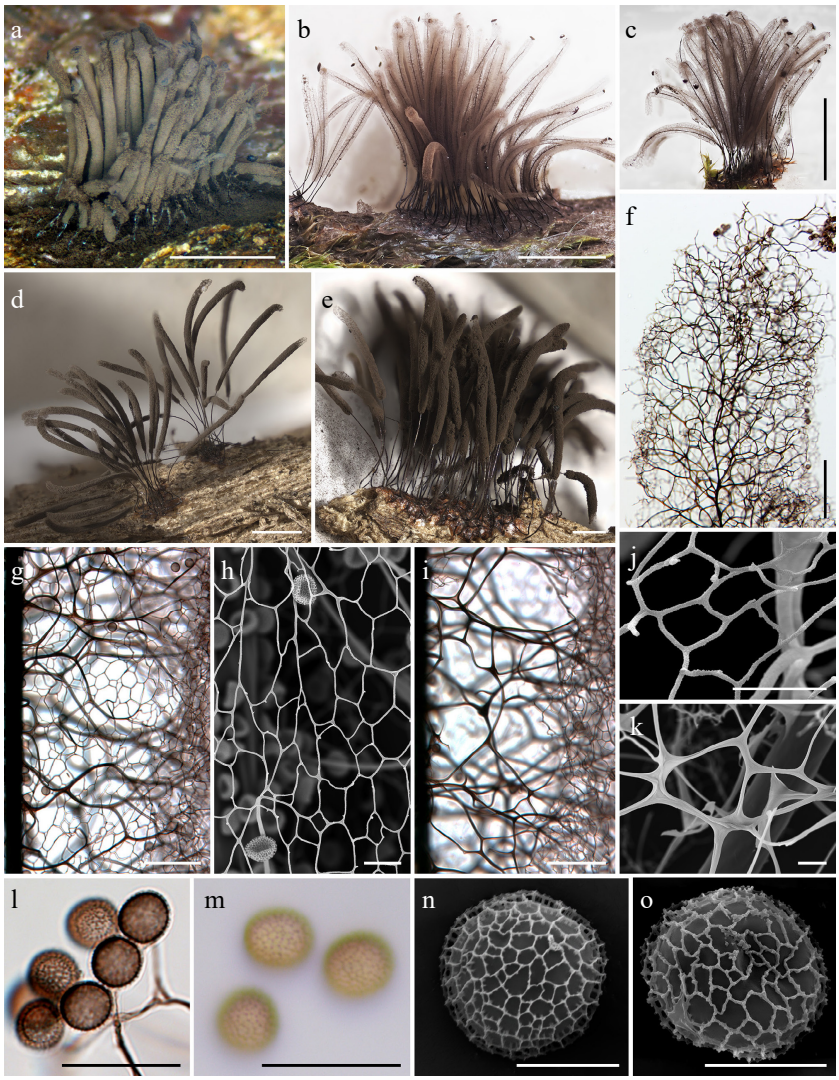

Fig. 19 Morphological characteristics of *Stemonitis* aff. *fusca* (a), (j), (m), (o) MYX 17763; (b), (f)–(i), (l), (n) MSK-F 43584; (c) HFNNU 12439; (d) LE348930; (e) LE348891; (k) MSK-F 43606. (a)–(e) Mature sporocarps (DM). (f) Apical region of the sporocarp (LM). (g) Surface net (LM). (h) Detail of the surface net (SEM). (i) Capillitium in the middle part of the sporotheca (LM). (j) Detail of the surface net (SEM). (k) Detail of the capillitium threads (SEM). (l), (m) Spores (LM). (n), (o) Spore (SEM). Scale bars: (a)–(d) = 2 mm; (e) = 1 mm; (f) = 100 μm; (g), (i) = 50 μm; (h,) (j)–(m) = 10 μm; (n), (o) = 5 μm.

MycoBank number: MB860493.

Synonym: *Stemonaria gracilis* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 87: 461 (1984).

Materials examined: **JAPAN**, Kochi Prefecture, Kochi-shi, Marunouchi High School, on bark of living *Cinnamomum camphora*, 18 Jul 1981, moist chamber, leg. Yamamoto Y. (holotype, TNS-M-Y-22046 = YY-1127). **RUSSIA**, Primorye Territory, Khasansky District, Kedrovaya Pad Nature Reserve, 43.0899° N, 131.4743° E, on litter, 29 Nov 2018, moist chamber, leg. Bortnikov F.M. (MYX 10257).

Notes: *Stemonitis gracilis* was originally described from Japan as *Sta. gracilis*[24] and was recently transferred to *Stemonitis* s.str. by Shchepin et al.[88]. This transfer was based on a specimen MYX 10257 identified as *Sta. gracilis* clustering within the *Stemonitis* s.str. clade (Fig. 1), and on the warted-reticulate spore ornamentation typical of that group.

Detailed examination of the holotype (TNS-M-Y-22046 = YY-1127; Fig. 21) provided new measurements that differ in part from the protologue. New measurements are: sporocarps 1.4–2.3(–2.6) mm in total height and 0.2–0.3 mm in width; stalk (0.5–)0.6–0.7 mm long (27%–43% of the total height); and spores (8.2–)9.1–9.5(–10.4) μm. While the spore diameter corresponds broadly to the protologue (9–10 μm), the sporocarps are markedly smaller than the protologue (2.5–3.5 mm). This discrepancy is likely due to the poor condition and scarcity (fewer than 10 sporocarps) of the holotype (Fig. 21c–f), which also precluded successful DNA extraction.

Morphologically, the holotype shows a dense capillitium (Fig. 21j, m, n), a very weak and incomplete surface net (Fig. 21k, l), and spores ornamented with a simple reticulate type with perforated muri, where the pillars distinctly surpass the muri tops and prominent perforations, with ca. 6–8 meshes across the spore diameter (Fig. 21q–t). This ornamentation confirms its placement in *Stemonitis* s.str., and this study therefore supports the transfer.

However, a detailed comparison in this study indicates that specimen MYX 10257 (Supplementary Fig. S5), used as the basis for the molecular placement by Shchepin et al.[88], is not conspecific with *Ste. gracilis*. Key differences include its much smaller sporocarps (barely reaching 1 mm in total height vs 2.5–3.5 mm in the protologue), slightly smaller spores (8–8.7(–8.8) μm in diameter vs 9–10 μm in the protologue), a finer, more abundantly branched capillitium and the presence of membranous expansions in the capillitium structures (Supplementary Fig. S5e), and a substrate of leaf litter in a moist chamber vs the bark of living trees recorded in

https://doi.org/10.48130/mycosphere-0026-0012

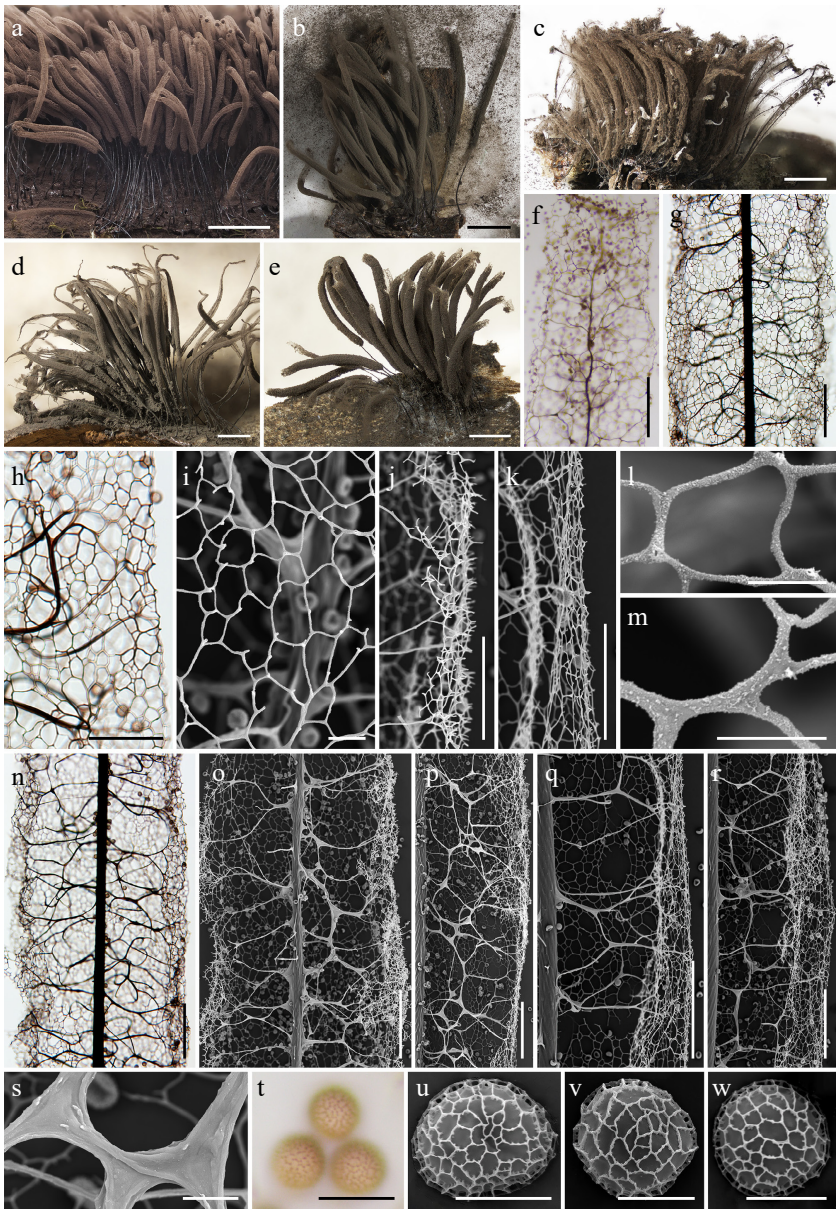

Fig. 20 Morphological characteristics of *Stemonitis fusca* agg. (a), (i), (j), (l), (o), (t) HFNNU 4212; (b) LE291133; (c) LE290927; (d) LE325855; (e) LE325706; (f), (t) MYX 19501; (g), (h), (k), (n), (q), (r), (w) LE328015; (m), (p), (s) LE346775; (v) MYX 19459. (a)–(e) Mature sporocarps (DM). (f) Apical region of the sporocarp (LM). (g), (h) Surface net (LM). (i) Detail of the surface net (SEM). (j), (k) Edge of the surface net (SEM). (l), (m) Detail of the surface net (SEM). (n) Capillitium in the middle part of the sporotheca (LM). (o)–(r) Capillitium in the middle part of the sporotheca (SEM). (s) Detail of the capillitium threads (SEM). (t) Spores (LM). (u)–(w) Spore (SEM). Scale bars: (a)–(e) = 2 mm; (f), (g), (n), (o)–(r) = 100 μm; (h), (j), (k) = 50 μm; (i), (s), (t) = 10 μm; (l), (m), (u)–(w) = 5 μm.

the protologue[24]. Critically, the spore ornamentation of specimen MYX 10257, although also of the simple reticulate type with perforated muri, is distinct in that the pillars do not surpass the tops of the muri (Supplementary Fig. S5f, g), contrasting with the condition in the holotype (Fig. 21s, t). Therefore, specimen MYX 10257 should be treated as *Ste.* aff. *gracilis*. Since the clade was formed by a single specimen, MYX 10257, with only a few sporocarps, this study refrains from describing it as a new species. However, future collections identical to MYX 10257 may warrant formal description.

The phylogenetic position of 'true' *Ste. gracilis* remains unresolved and awaits the study of unambiguously identified fresh material. Consequently, the records of *Ste. gracilis* require critical revision; for example, the illustration in Lado et al.[107] differs significantly from both the protologue and re-examination of the holotype (Fig. 21).

***Stemonitis imperfecta* W.L. Song, M.L. Cai & Shuang L. Chen, sp. nov. Fig. 22**

MycoBank number: MB863120.

Etymology: *imperfecta* (Latin) imperfect, incomplete, unfinished; from *in*-(not) and *perfectus* (completed, perfect), referring to the incomplete surface net of this species.

Holotype: CHINA, Shanghai City, Haiwan National Forest Park, 30.8719° N, 121.7138° E, on bark of living tree, 2 Sep 2025, moist chamber, leg. Cai M.L. (HFNNU 12493, GenBank *nrSSU*: PX940062).

Diagnosis: Sporocarps measuring (1.9–)2.2–2.8(–3.9) mm in total height, loosely gregarious; surface net sparse and incomplete, with meshes measuring (8.9–)16.4–31.2(–64.7) μm in diameter; spore (9.1–)9.6–10.3(–11.2) μm in diameter, ornamented with a simple reticulate type with perforated muri, sometimes incomplete, characterized by pillars distinctly surpassing the muri tops, numbering about 7–10 across the diameter.

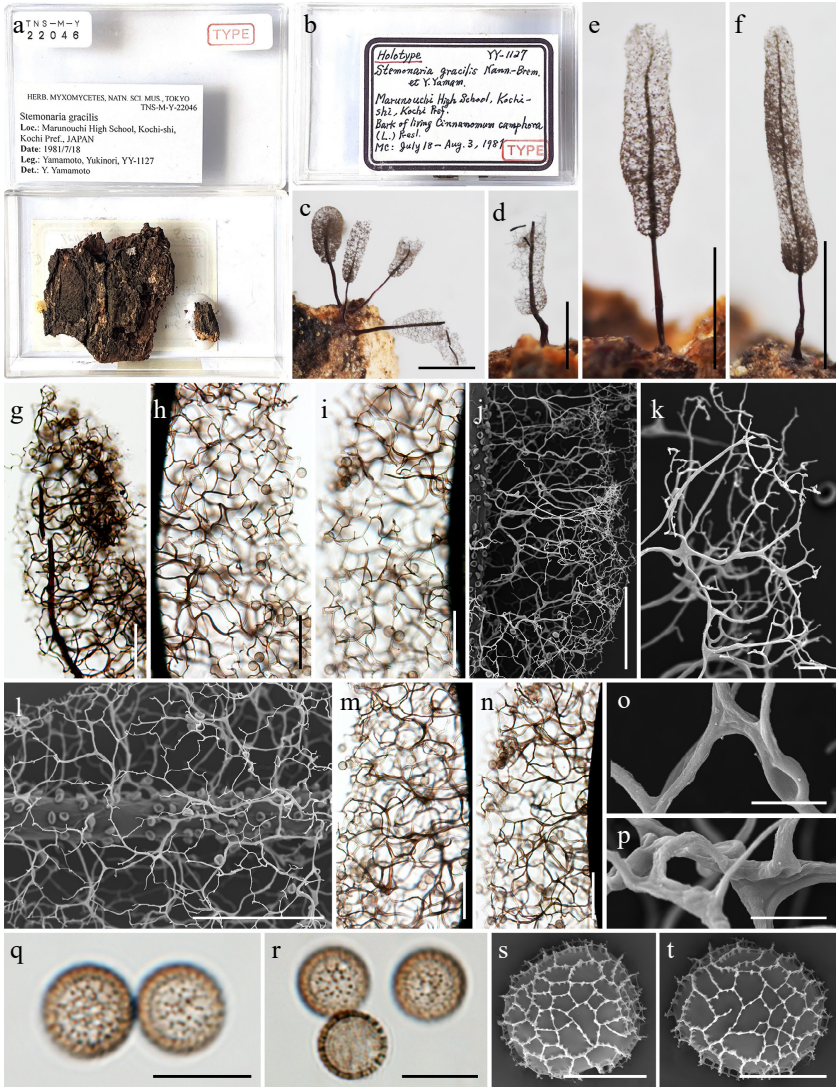

Fig. 21 Morphological characteristics of the holotype (TNS-M-Y-22046 = YY-1127) of *Stemonitis gracilis* (≡ *Stemonaria gracilis*). (a) Herbarium labels and interior views of the herbarium box containing the holotype. (b) Herbarium labels of the herbarium box containing the holotype. (c)–(f) Mature sporocarps (DM). (g) Apical view of the sporotheca (LM). (h), (i) Surface net in the middle part of the sporotheca (LM). (j) Capillitium and surface net in the middle part of the sporotheca (SEM). (k) Capillitium and surface net in the edge of the sporotheca (SEM). (l) Surface net (SEM). (m), (n) Capillitium in the middle part of the sporotheca (LM). (o), (p) Detail of the capillitium threads (SEM). (q), (r) Spores (LM). (s), (t) Spore (SEM). Scale bars: (c)–(f) = 1 mm; (g), (j), (l) = 100 μm; (h), (i), (m), (n) = 50 μm; (k), (o)–(r) = 10 μm; (s), (t) = 5 μm.

Description: Sporocarps erect, stalked, loosely gregarious, (1.9–)2.2–2.8(–3.9) mm in total height. Sporotheca elongate-cylindrical, tapering towards both ends, apex bluntly rounded, dark brown, (0.1–)0.2–0.3 mm wide. Stalk black, shiny, (0.4–)0.6–0.8(–1.0) mm long, 20%–36% of the total height, base forming a short cone. Hypothallus membranous, black to moderate brown to moderate orange, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex as a slender filament. Capillitium arising perpendicularly from the entire length of the columella, dark reddish-orange, with a triangular expansion at the point of origin, much-branched; branching points with inconspicuous membranous expansions, often smoothly rounded, threads nearly smooth, connecting to the surface net or forming free ends. Surface net poorly developed, incomplete, more complete in the middle of the sporotheca; meshes irregularly polygonal to subcircular, of unequal diameter, (9–)16–31(–65) μm, bearing spines of variable length; threads nearly smooth. Spore concolorous with the sporotheca in mass, reddish brown or lighter in transmitted light, globose to subglobose, (9.1–)9.6–10.3(–11.2) μm in diameter, ornamented with a simple reticulate type with perforated muri, sometimes incomplete, characterized by sparse and unequal meshes, numbering about 7–10 across the diameter, pillars distinctly surpassing the tops of the muri, and prominent perforations. Plasmodium not observed.

Additional materials examined: CHINA, Shanghai City, Haiwan National Forest Park, 30.8719° N, 121.7138° E, on bark of living tree, 30 Aug 2025, moist chamber, leg. Cai M.L. (HFNNU 12492); Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, 32.0682° N, 118.8791° E, on bark of living tree, 4 Jul 2023, moist chamber, leg. Lin D. and Song W.L. (HFNNU 8808).

Distribution: currently known from Eastern China, probably occurs in Far Eastern Russia.

Habitat: on bark of living tree.

Notes: One unvouchered specimen with spores similar in size and ornamentation was observed in Primorye Territory in a moist chamber on the bark of a living *Abies holophylla* (pH = 5.1), which may indicate a wider distribution of this species in the Asian region.

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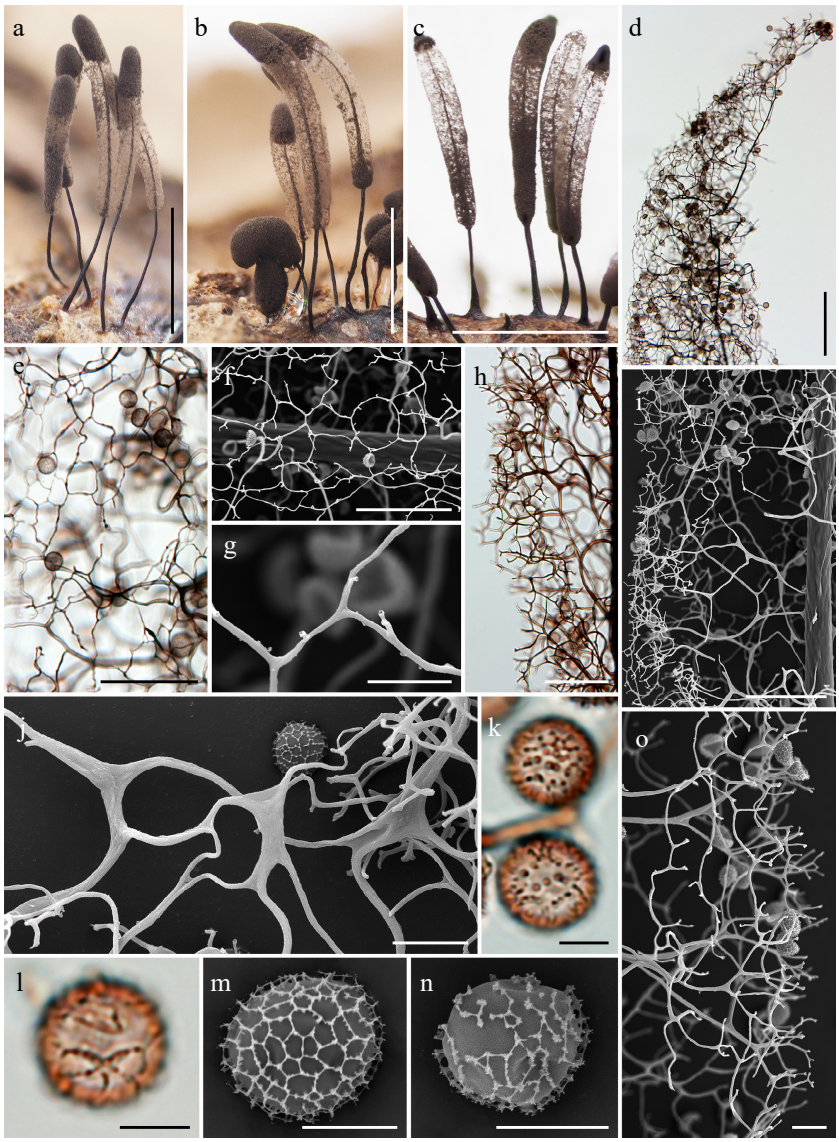

Fig. 22 Morphological characteristics of *Stemonitis imperfecta* (a), (b), (f)–(o) HFNNU 8808; (c)–(e) HFNNU 12493. (a)–(c) Mature sporocarps (DM). (d) Apical region of the sporocarp (LM). (e) Surface net (LM). (f), (g) Detail of the surface net (SEM). (h) Capillitium in the middle part of the sporotheca (LM). (i) Capillitium in the middle part of the sporotheca (SEM). (j) Detail of the capillitium threads (SEM). (k), (l) Spores (LM). (m), (n) Spore (SEM). (o) Edge of a sporotheca (SEM). Scale bars: (a)–(c) = 1 mm; (d) = 200 μm; (e), (f), (h), (i) = 50 μm; (g), (j), (o) = 10 μm; (k)–(n) = 5 μm.

Morphologically, *Ste. imperfecta* is similar to *Ste. pinicola* (≡ *Stp. amoena*), sharing a comparable growth habit (*Pinus* sp. bark), sporocarp size, stalk proportion, and an incomplete surface net. However, *Ste. pinicola* has distinctly smaller spores (6.0–7.5 μm in diameter)[23]. *Stemonitis imperfecta* also resembles *Ste. marjana*, which was described as having an irregular spore reticulum and spores measuring 8.8–9.8 μm in diameter. A re-examination of the holotype of *Ste. marjana* in the present study, however, revealed a rather regular reticulum characterized by pillars not exceeding the tops of the muri. Furthermore, *Ste. marjana* possesses a shorter stalk (15%–20% of the total height) and a robust columella that reaches the sporotheca apex, whereas in *Ste. imperfecta* the stalk comprises 20%–36% of the height and the columella terminates as a slender filament at the apex (Fig. 22d), suggesting the two are distinct. *Stemonitopsis reticulata* (H.C. Gilbert) Nann.-Bremek. & Y. Yamam. shows some resemblance but differs in its longer stalk (ca. half the total height), although the spore diameter of *Stp. reticulata* was recorded as 7–9 μm in its protologue[108]. The type specimen was examined by Farr[109], who confirmed the smaller spore size. The specimen reported as *Stp. reticulata* by Yamamoto and Nannenga-Bremekamp[91] with 9–10 μm spores likely represents a different taxon, highlighting the need for further revision of this species complex.

Phylogenetically, *Ste. imperfecta* forms a well-supported clade sister to *Ste.* cf. *foliicola* (UBS/PP/TBE = 98/-/84; Fig. 1). However, *Ste. imperfecta* is morphologically distinct from *Ste.* cf. *foliicola*, which has a complete surface net (Fig. 18g, m, n), a denser, more regular capillitium (Fig. 18f, h, k, l), and smaller spores measuring (6.7–)7.8–8.7(–9.8) μm in diameter (Fig. 18p, q). Based on this unique combination of morphological and phylogenetic evidence, *Ste. imperfecta* is recognized as a previously undescribed species.

***Stemonitis liaoningensis* (B. Zhang & Yu Li) Bortnikov, W.L. Song & Novozh., comb. nov.**

MycoBank number: MB863326.

Basionym: *Stemonaria liaoningensis* B. Zhang & Yu Li, Sydowia 64(2):331 (2012).

Notes: *Stemonaria liaoningensis* is known only from Liaoning Province, China, and was described based on a single, poorly preserved specimen[93]. Its reported characteristics include: small sporocarps (2.3–2.5 mm in total height) with a stalk about half the total height, a dense capillitium with numerous membranous extensions, an incomplete surface net, and warted-reticulate spores 7–10 μm in diameter with 5–8 meshes across the diameter. The SEM images in the protologue suggest a spore ornamentation of connected warts with perforated plates[93], which would place *Stemonitis* as *Ste. liaoningensis*. However, the poor image resolution and the specimen's condition make confident assessment difficult; the ornamentation somewhat resembles that of *Stemonitopsis hyperopta* (Meyl.) Nann.-Bremek., though the latter typically has smaller spores and a different mesh structure. Consequently, the species' validity and precise relationships remain unclear.

The protologue compares the taxon exclusively with species of *Stemonaria*[93], but it should also be considered alongside other *Stemonitis* species that lack a well-developed surface net, such as *Ste. reticulospora* (≡ *Com. reticulospora*), which shares small sporocarp size (2.0–2.5 mm in total height), dense capillitium, and spores 6–10 μm in diameter, though its spores appear more coarsely reticulate with ca. 4–6 meshes across the diameter[94], thus these two species, which have not yet been confirmed by new findings and high-quality illustrations of type specimens, should be considered together, as they appear to be easily confused.

***Stemonitis longa* (Peck) Massee, A Monograph of the Myxogastres: 83 (1892)**

MycoBank number: MB379136.

Synonyms: *Comatricha longa* Peck, Rep. (Annual) New York State Mus. Nat. Hist. 43: 70 (1890).

Synonyms: *Stemonaria longa* (Peck) Nann.-Bremek., R. Sharma & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 87: 453 (1984).

Materials examined: BELARUS, Minsk Region, Myadzyel District, Narachanski National Park, vicinity of Yatsyny village, 54.9490° N, 26.4631° E, on rotten wood, 10 Sep 2024, field, leg. Moroz E.L. (MSK-F 43585). **CHINA**, Jiangxi Province, Yichun City, Guan Mountain National Nature Reserve, on rotten wood, 17 Jul 2022, field, leg. Chen S.L. and Yan S.Z. (HFNNU 4171, HFNNU 4172); Jiangxi Province, Pingxiang City, Bihutan National Forest Park, on rotten wood, 15 Jul 2022, field, leg. Chen S.L. and Yan S.Z. (HFNNU 4190); Guangdong Province, Zhaoqing City, Dinghu Mountain National Nature Reserve, on rotten wood, 29 May 2014, field, leg. Wei B. and He G. (HFNNU 1233, HFNNU 12491); Henan Province, Xinyang City, Dongzhai National Nature Reserve, 31.4541° N, 114.2015° E, on rotten wood, 17 Aug 2020, field, leg. Du Q. (HMAS 0294768); Henan Province, Xinyang City, Jigong Mountain National Nature Reserve, 32.1311° N, 114.0692° E, on litter, 10 Nov 2020, field, leg. Du Q. (HMAS 0294858). **RUSSIA**, Republic of Tatarstan, Zelenodolsky District, vicinity of Urnyak village, 55.8581° N, 48.7583° E, on decayed bark of *Quercus robur*, 10 Oct 2017, moist chamber (pH = 5.95), leg. Zemlyanskaya I.V. (LE278859); Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.9055° N, 37.5588° E, on rotten wood, 2 Oct 2024, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 24803). **VIETNAM**, Binh Phuoc Province, Bù Gia Mập District, Bù Gia Mập National Park, 12.1906° N, 107.2104° E, on a finally decayed log of *Pinus krempfii*, 28 Nov 2017, field, leg. Popov E.S. (LE317506).

Notes: The combination *Ste. longa* was originally proposed by Massee[110], but was not accepted by most authors[13,111]. In the work of Shchepin et al.[88], sequences of this species, which occupies a place within the clade *Stemonitis* s.str., were studied. The present results confirm the presence of this species within *Stemonitis* s.str. (Fig. 1). This is a very widespread species with characteristic morphology. Its distinctive characteristics are large, drooping, often merged, very long sporothecae on short stalks, a fairly loose capillitium, and reticulate spores[13]. Sporocarps are formed on rotten wood, but they can often be found on old perennial fruiting bodies of polypore fungi.

***Stemonitis longoides* Bortnikov, Novozh., Gmoshinskiy & W.L. Song, nom. nov.**

MycoBank number: MB863327.

Synonym: *Stemonaria reticulospora* Nann.-Bremek., R. Sharma & K.S. Thind, Proc. Kon. Ned. Akad. Wetensch., C 87: 451 (1984) non *Comatricha reticulospora* Ing & P.C. Holland, Trans. Brit. Mycol. Soc. 50 (4): 685 (1967).

Etymology: Greek suffix -οειδής (-oeidēs), meaning 'resembling' or 'like'. The name was chosen to highlight the similarity of this taxon to species of the former *Stemonaria*, including *Ste. longa*, that have also been moved from *Stemonaria* to *Stemonitis*.

Notes: *Stemonaria reticulospora* was originally described from India[24]. It is characterized by long dark brown sporocarps (7–8 mm in total height), the absence of a surface net, and small spores (6.0–6.5[–7.0] μm in diameter), with warted-reticulate ornamentation. To our knowledge, no further collections have been reported, and the type specimen has not been re-examined in any subsequent revision. Nevertheless, the presence of warted-reticulate spores places this species unequivocally within *Stemonitis* s.str. as circumscribed in this study, and the new combination is proposed accordingly.

***Stemonitis marjana* Y. Yamam., Karstenia 40(1-2): 197 (2000), Fig. 23**

MycoBank number: MB466153.

Materials examined: JAPAN, Kochi Prefecture, Kochi-shi, Otsu, Seki, on ligno carioso *Pinus densiflora*, 20 Aug 1987, field, leg. Yamamoto Y. (holotype, TNS-M-Y-22054 = YY-5887).

Notes: *Stemonitis marjana* was described from Japan[112]. Examination of the holotype (TNS-M-Y 22054 = YY-5887; Fig. 23) revealed it to be in poor condition and heavily contaminated with fungi, preventing successful DNA extraction. New measurements of the holotype are as follows: sporocarps (2.9–)3.1–3.3(–3.4) mm in total height and 0.3–0.4 mm in width; stalk 0.5–0.6(–0.7) mm long (15%–20% of the total height); and spores (8.5–)9.1–10.2(–10.9) μm in diameter. These values largely correspond to the protologue (sporocarps 2.1–2.9 mm in total height and 0.18–0.25 mm wide, stalk 0.5–0.7 mm long, 2/10–3/10 of the total height, and spores 8.8–9.8 μm in diameter). Due to the specimen's degraded state, the surface-net diameter could not be reliably measured (Fig. 23f, g). Detailed morphological study revealed several diagnostic characteristics: columella apex is variable, curved, branched, or filamentous (Fig. 23d, e); capillitium is relatively sparse, with threads bearing abundant small warts (Fig. 23e, f, l); surface net has sparse meshes, its threads also warted (Fig. 23f, g, j, k); and spores ornamented with a simple reticulate type with perforated muri, with pillars not exceeding the muri tops (Fig. 23h, i). This ornamentation type aligns with the circumscription of *Stemonitis* s.str., supporting the placement of the species within this clade. Morphologically, *Ste. marjana* is similar to the newly described *Ste. imperfecta* in this study, as they share comparable sporocarp and spore dimensions. They are distinguished, however, by consistent differences in spore ornamentation (pillars not exceeding vs distinctly surpassing the muri tops) and stalk proportion (15%–20% vs 20%–36% of the total height; see Notes for *Ste. imperfecta*).

Zhang & Li[113] reported this species based on specimen HMJAU 10431 collected from Jilin Agricultural University. However, the photograph provided (see Zhang & Li[113]: fig. 2) shows several

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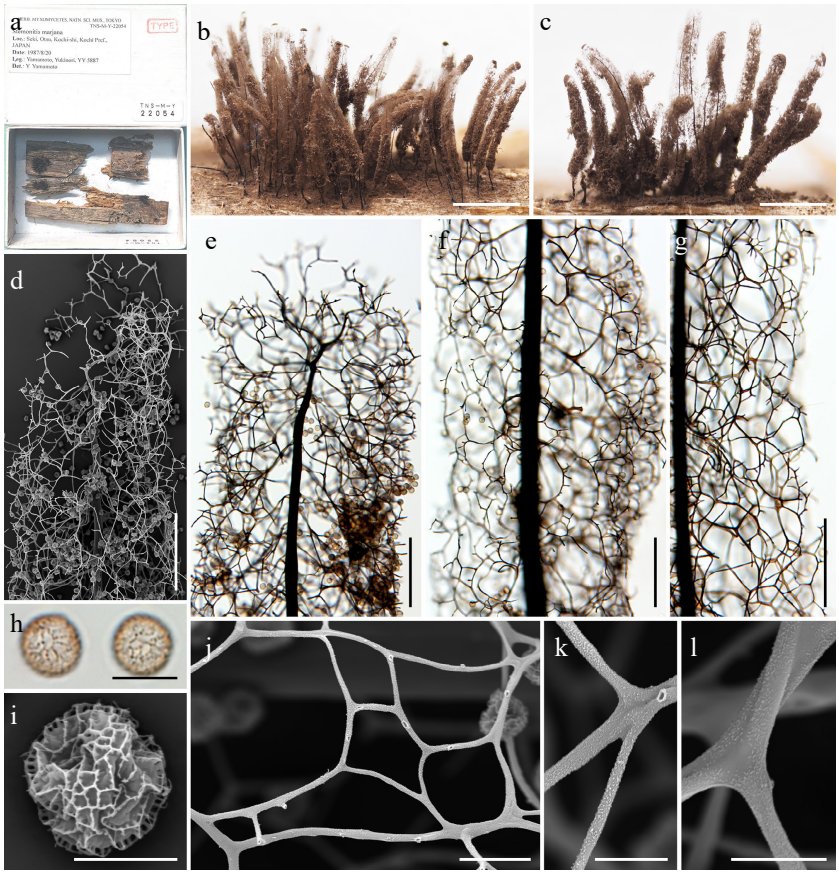

Fig. 23 Morphological characteristics of the holotype (TNS-M-Y-22054 = YY-5887) of *Stemonitis marjana*. (a) Herbarium label and interior view of the herbarium box containing the holotype. (b), (c) Mature sporocarps (DM). (d) Apical view of the sporotheca (SEM). (e) Apical view of the sporotheca (LM). (f), (g) Surface net (LM). (h) Spores (LM). (i) Spore (SEM). (j), (k) Detail of the surface net (SEM). (l) Detail of the capillitium threads (SEM). Scale bars: (b), (c) = 1 mm; (d)–(g) = 100 μm; (h), (j) = 10 μm; (i), (k), (l) = 5 μm.

discrepancies with the holotype and the protologue: the stalk (1–1.5 mm) is considerably longer; the surface net and capillitium are denser; and the spores have a denser and smaller diameter. Therefore, the identification as *Ste. marjana* is considered to be incorrect. Further re-examination of this specimen is required.

***Stemonitis minuta* (Nann.-Bremek. & Y. Yamam.) W.L. Song, Bortnikov, Novozh. & Shuang L. Chen, comb. nov. Fig. 24**

MycoBank number: MB863328.

Basionym: *Stemonaria minuta* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 90: 347 (1987).

Materials examined: JAPAN, Kochi Prefecture, Aki-shi, Enokawa-naka Park, on dead wood of *Podocarpus macrophylla*, 6 Jul 1985, field, leg. Yamamoto Y. (isotype, TNS-M-Y-22049 = YY-2961).

Notes: *Stemonaria minuta* was described from Japan[114]. Examination of the isotype (TNS-M-Y-22049 = YY-2961; Fig. 24) provided new morphological data: sporocarps (1.1–)1.2–1.6(–1.8) mm in total height and 0.3–0.4 mm in width; stalk 0.2–0.3(–0.4) mm long (14%–27% of the total height); and spores (8.7–)9.3–9.9(–10.6) μm in diameter. These values are largely consistent with the protologue, which reported sporocarps (0.6–)0.8–1.2 mm in total height, 0.2–0.4 mm in diameter, a very short stalk (1/9–1/7 of the total height), and spores ca. 10 μm in diameter.

The most distinctive characteristic of *Sta. minuta* is the spore ornamentation. The protologue describes it as 'palely, minutely warted or spinulose, … forming an irregular, delicate net with many elongate meshes'[114]. Detailed SEM reveals it conforms to the simple reticulate type with perforated muri (Fig. 24l, m). The pillars are distinct, arranged in aligned rows, and surpass the muri tops; the perforations are conspicuous, and the meshes are often elongated yet closed (Fig. 24l, m). This combination of aligned pillars and elongated closed meshes appears to be unique within Stemonitidales. As this reticulate spore ornamentation aligns with the circumscription of *Stemonitis* s.str., *Sta. minuta* is transferred to *Stemonitis* as *Ste. minuta*.

The columella also shows variation: in addition to the originally described 'flexuose tip'[114] dissipating near the apex, it sometimes terminates in a small, funnel-shaped structure (Fig. 24d) and may be irregularly swollen at the base of the sporotheca (Fig. 24f). Unfortunately, due to the age of the isotype, DNA extraction and sequencing were unsuccessful. Therefore, the phylogenetic position of *Ste. minuta* remains unresolved.

***Stemonitis palustris* W.L. Song, Bortnikov, Shuang L. Chen & Novozh., sp. nov. Fig. 25**

MycoBank number: MB863123.

Etymology: *palustris* (Latin) of marshes, swampy; from *palus*, *paludis* (a marsh, swamp), referring to the typical habitat of this species, which is found in wet, boggy, or marshy environments.

Holotype: RUSSIA, Leningrad Region, Vyborgsky District, Bolshoy Beryozovy Island, 60.2929° N, 28.6806° E, on mosses, 6 Sep 2024, field, leg. Novozhilov Yu.K. and Luptakova A.D. (LE346780, GenBank *nrSSU*: PX940057; *EF-1α*: PX961591).

Diagnosis: Sporocarps measuring 3.3–4.5 mm in total height, in dense tufts; stalk short, about 15%–25% of the total height; surface net well-developed; spores (8.1–)9.1–9.8(–11.0) μm in diameter,

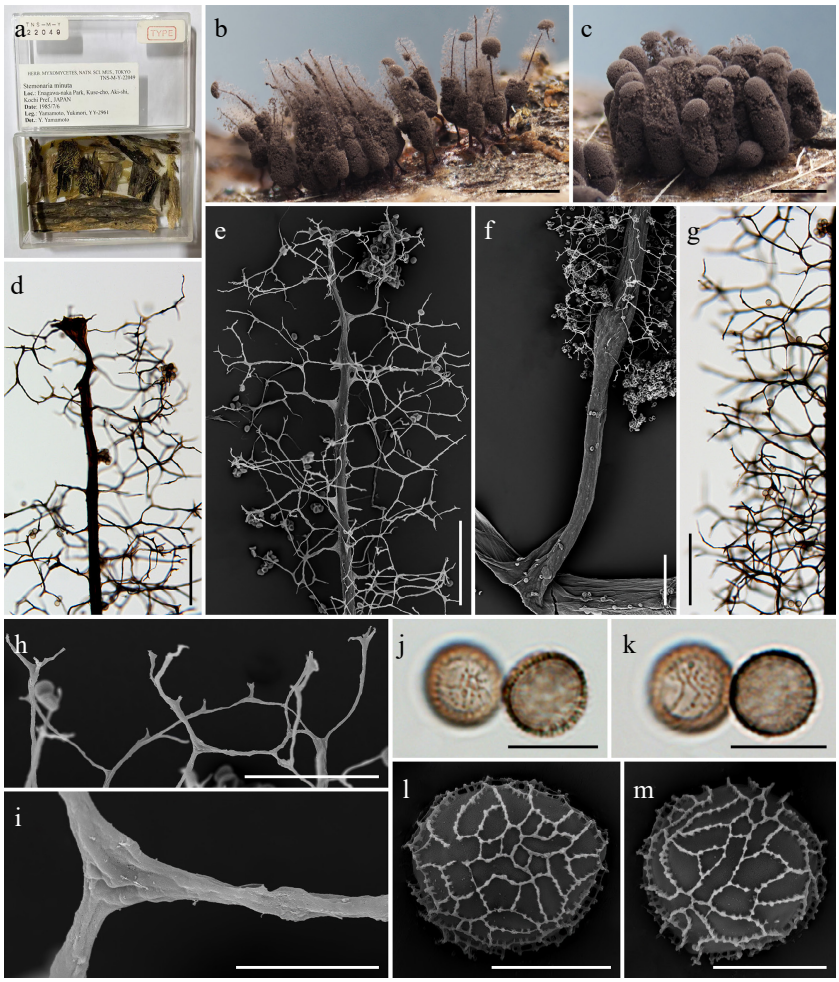

Fig. 24 Morphological characteristics of the isotype (TNS-M-Y-22049 = YY-2961) of *Stemonitis minuta* (≡ *Stemonaria minuta*). (a) Herbarium label and interior view of the herbarium box containing the holotype. (b), (c) Mature sporocarps (DM). (d) Apical view of the sporotheca (LM). (e) Apical view of the sporotheca (SEM). (f) Stalk (SEM). (g) Capillitium in the middle part of the sporotheca (LM). (h) Edge of the sporotheca (SEM). (i) Detail of the capillitium threads (SEM). (j), (k) Spores (LM). (l), (m) Spore (SEM). Scale bars: (b), (c) = 0.5 mm; (d)–(g) = 100 μm; (h) = 50 μm; (i)–(k) = 10 μm; (l), (m) = 5 μm.

ornamented with a simple reticulate type with perforated muri, low pillars not exceeding the muri tops, meshes numbering about 7–9 across the spore diameter.

Description: Sporocarps erect, stalked, densely gregarious, (3.3–)3.6–4.2(–4.5) mm in total height. Sporotheca cylindrical, slightly tapering at both ends, apex bluntly rounded, dark brown, 0.3–0.4 mm wide. Stalk black, shiny, (0.5–)0.6–0.9(–1.1) mm long, 15%–25% of the total height, base forming a short cone. Hypothallus membranous, deep brown to moderate brown, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex, often sinuous at the apex. Capillitium arising from the entire length of the columella, black to dark brown, with a triangular membranous expansion at the point of origin, dense, much and intricately branched, with membranous expansions at the branching points, threads nearly smooth but bearing some irregular, large warts, connecting to the surface net. Surface net well-developed, often incomplete at the sporotheca apex but complete elsewhere, threads filamentous, slightly sinuous, meshes irregularly polygonal to circular, (6–)8–14(–25) μm in diameter, threads densely covered with irregular small warts, irregularly bearing spines of variable length. Spore concolorous with the sporotheca in mass, reddish orange to brown in transmitted light, globose to subglobose, (8.1–)9.1–9.8(–11.0) μm in diameter, ornamented with a simple reticulate type with perforated muri, characterized by sparse meshes, numbering about 7–9 across the spore diameter, low pillars not exceeding the tops of the muri, and prominent perforations. Plasmodium not observed.

Distribution: currently known from European Russia (Leningrad Region).

Habitat: on *Sphagnum* mosses.

Notes: *Stemonitis palustris* belongs to the group of *Stemonitis* species with small sporocarps 3.3–4.5 mm in total height (Fig. 25a, b). This group also includes *Ste. curvicornis*, *Ste. foliicola*, *Ste. imperfecta*, *Ste. pinicola* (≡ *Stp. amoena*), *Ste. pinnatiapicalis*, *Ste. spinimuralis*, and *Ste. virginiensis*. Among these, two litter-inhabiting species, *Ste. foliicola*[102] and *Ste. spinimuralis*, are distinguished by smaller spores (7.0–8.0 μm and 7.9–8.5 μm, respectively, compared to 9.1–9.8 μm in *Ste. palustris*). The wood-inhabiting species in this group also have smaller spores: *Ste. virginiensis* (5.5–6.5 μm)[71,100], *Ste. pinicola* (6.0–7.6 μm)[23,115], *Ste. pinnatiapicalis* (7.8–8.6 μm), and *Ste. curvicornis* (8.2–8.7 μm; Fig. 15). Additionally, *Ste. curvicornis* (Fig. 15n), *Ste. imperfecta* (Fig. 22m, n), *Ste. pinnatiapicalis*, and *Ste. spinimuralis* differ from *Ste. palustris* in having pillars that distinctly exceed the muri tops under SEM, a characteristic absent in *Ste. palustris* (Fig. 20k). Although *Ste. imperfecta* also has relatively large spores (9.6–10.3 μm), it is easily distinguished by its incomplete reticulation with breaks in the ornamentation. Phylogenetically, *Ste. palustris* forms an independent branch within the *Stemonitis* s.str.

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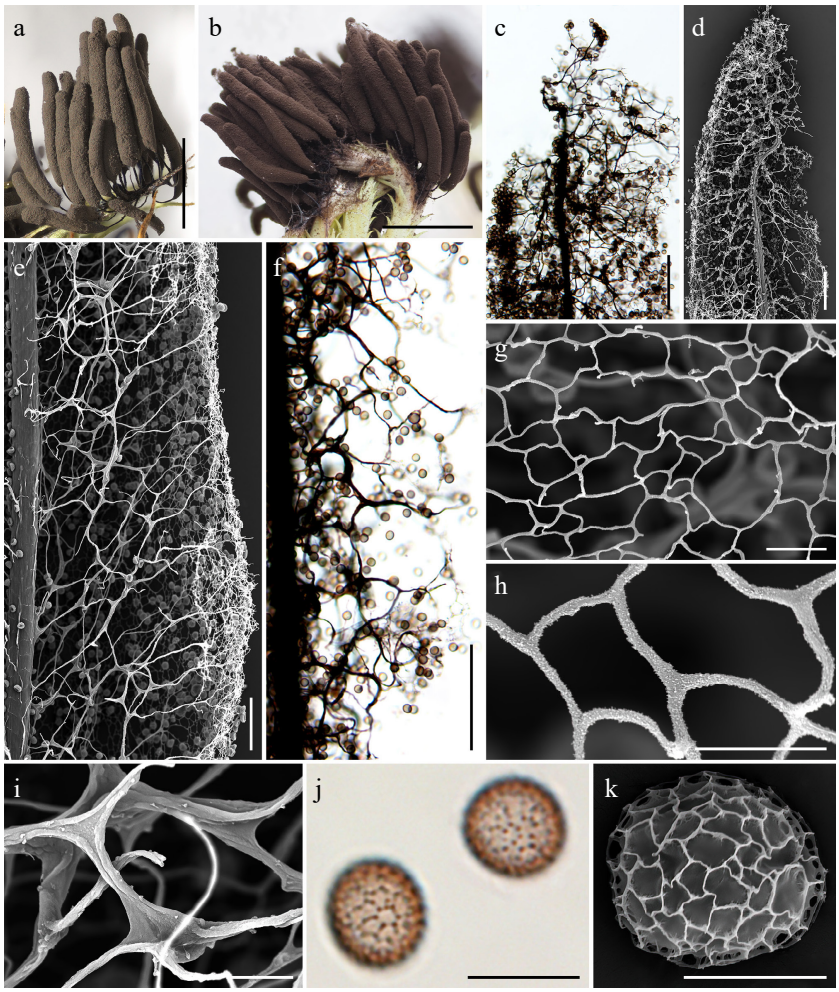

Fig. 25 Morphological characteristics of *Stemonitis palustris* (LE346780). (a), (b) Mature sporocarps (DM). (c) Apical region of the sporocarp (LM). (d) Apical region of the sporocarp (SEM). (e) Capillitium in the middle part of the sporotheca (SEM). (f) Capillitium in the middle part of the sporotheca (LM). (g), (h) Detail of the surface net (SEM). (i) Detail of the capillitium threads (SEM). (j) Spores (LM). (k) Spore (SEM). Scale bars: (a), (b) = 2 mm; (c), (d), (f) = 100 μm; (e) = 50 μm; (g), (i), (j) = 10 μm; (h), (k) = 5 μm.

clade, showing no sister-group relationship with other known species (Fig. 1). The stable morphological differences outlined above, combined with its distinct phylogenetic position, further support the recognition of *Ste. palustris* as an independent new species.

While describing a new taxon based on a single collection is atypical, the holotype of *Ste. palustris* consists of a large and well-developed colony, providing ample and reliable material for morphological evaluation. The stable morphological differences outlined above, combined with its distinct phylogenetic position, support its recognition as an independent new species. Furthermore, as the type locality is situated in a region routinely surveyed by the authors, additional collections are anticipated in the future to supplement the data for this species.

Stemonitis pilosa **(Nann.-Bremek.) Bortnikov, W.L. Song, Gmoshinskiy, Shuang L. Chen & Novozh., comb. nov. Fig. 26**

MycoBank number: MB863329.

Basionym: *Stemonaria pilosa* Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C 87: 455 (1984).

Materials examined: BELARUS, Minsk Region, Minsk District, Glebkovka Reserve, vicinity of Kolodishchi village, 53.9322° N, 27.8071° E, on rotten wood, 28 Oct 2023, field, leg. Moroz E.L. (MSK-F 43540). **RUSSIA**, Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.9214° N, 158.7158° E, on decayed log of *Salix udensis*, 11 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325048); Vladimir Region, Sudogodsky District, vicinity of Lobanovo village, 56.0166° N, 40.8122° E, on rotten wood, 10 Nov 2021, field, leg. Mishulin A.A. and Gmoshinskiy V.I. (MYX 19510); Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.8976° N, 37.5654° E, on rotten wood, covered by moss, 08 Jul 2022, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 20696); Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.9009° N, 37.5583° E, on rotten wood, covered by moss, 12 Jul 2024, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 24292); Sverdlovsk Region, Krasnoufimsky, vicinity of Krasnosokolye village, 56.9224° N, 57.4508° E, on rotten wood and bark, 27 Aug 2024, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 24418).

Notes: *Stemonaria pilosa* was described from Sweden[24] and has been seldom reported since. The protologue describes the spore ornamentation as a distinct reticulum formed rows of free small spines, producing fine meshes[24], a pattern characteristic of *Stemonitis* s.str. Therefore, it is transferred to *Stemonitis* s.str. under the new combination *Ste. pilosa*.

The specimens studied here match the protologue[24] in several key characteristics: it has a similar habit with sporocarps ca. 9.5 mm in total height; a stalk constituting nearly half of the total height

(e.g., 43% in LE325048), a proportion uncommon in larger *Stemonitis* s.l.; and spores measuring (7.0–)7.4–8.3(–8.9) μm, practically identical to the protologue (7–8.5 μm). The very loose capillitial network with long free ends, noted in the original description, is also present in the examined material (Fig. 26e, g, j, k). Rounded, bubble-like thickenings on the capillitial threads, as illustrated in the original figure, are observed in specimens MYX 24418, MYX 19510, and LE325048 (Fig. 26e, h, i). Nevertheless, these bubble-like structures are considered unstable for species delimitation. Although similar structures are diagnostic for *Macbrideola vesiculifera* Novozh. (= *Macbrideola cornea* [G. Lister & Cran] Alexop.)[116], they may instead arise from morphogenetic disturbances during sporocarp development. This interpretation is supported by the observation that non-vesiculate sporotheca of *M. cornea* occur under identical conditions.

Phylogenetically, the specimens form a well-supported sister branch with *Ste. amphorocolumella* NSK 1026087 (UBS/PP/TBE = 100/100/100; Fig. 1). Given that members of this clade are predominantly European (the sole exception being LE325048 from Kamchatka), and the type of *Ste. pilosa* has not been re-examined in detail, this study refrains from describing the studied specimens as new, and they are therefore tentatively identified as *Ste.* cf. *pilosa*. Future studies should re-examine the type and morphologically similar specimens to confirm or refine this preliminary determination.

***Stemonitis pinicola* Shchepin, Prikhodko, Gmoshinskiy, Schnittler & Novozh.**

MycoBank number: MB860495.

Synonyms: *Comatricha amoena* Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C 71: 45 (1968).

Synonyms: *Stemonitopsis amoena* (Nann.-Bremek.) Nann.-Bremek., De Nederlandse Myxomyceten: 205 (1975).

Notes: *Stemonitis pinicola* was originally described as *Com. amoena* from a dead pine trunk in the Netherlands[115] and then revised to *Stp. amoena*[23]. It is characterized by small, dark brown sporocarps (2.0–3.5 mm in total height, ca. 0.5 mm in diameter), a well-defined capillitium with an incomplete surface net, and reticulate spores 6–7 μm in diameter; the reticulum consists of rows of spinules, with five or six meshes across the diameter. Nannenga-Bremekamp[115] noted the similarity of its spore ornamentation to

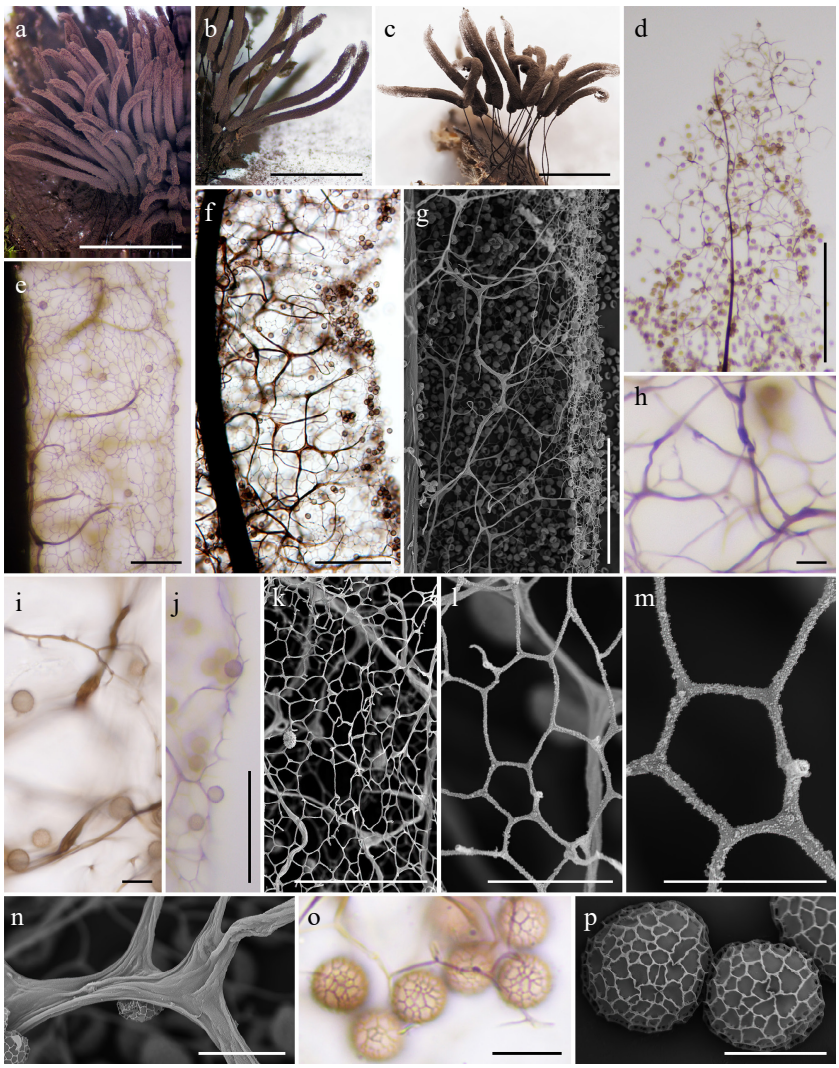

Fig. 26 Morphological characteristics of *Stemonitis* cf. *pilosa* (a), (d), (h), (o) MYX 24292; (b) MYX 20696; (c), (f), (g), (i), (k)–(n), (p) LE325048; (e), (j) MYX 24418. (a)–(c) Mature sporocarps (DM). (d) Apical view of the sporotheca (LM). (e) Surface net (LM). (f) Capillitium in the middle part of the sporotheca (LM). (g) Capillitium in the middle part of the sporotheca (SEM). (h), (i) Rounded thickenings in the capillitium (LM). (j) Edge of the sporotheca (LM). (k)–(m) Detail of the surface net (SEM). (n) Detail of the capillitium threads (SEM). (o) Spores (LM). (p) Spores (SEM). Scale bars: (a)–(c) = 5 mm; (d)–(g), (j) = 100 μm; (k) = 50 μm; (h), (i), (l), (n), (o) = 10 μm; (m), (p) = 5 μm.

that of *Ste. fusca*. The species was subsequently transferred to *Stemonitis* as *Ste. pinicola*[88]. The type of this species has not been examined, and SEM images are unavailable. Interpretations of the species appear to vary among authors[18,63,64,72,106], suggesting that the name *Stp. amoena* (≡ *Ste. pinicola*) may be applied to different, closely related taxa. Examination of the type material is required to clarify the morphology of the 'true' *Ste. pinicola*.

***Stemonitis pinnatiapicalis* W.L. Song, Gmoshinskiy, Bortnikov, Novozh. & Shuang L. Chen, sp. nov. Fig. 27**

MycoBank number: MB863121.

Etymology: *pinnatiapicalis* (Latin) with a feather-like (pinnate) apex, from *pinnatus* (feathered, pinnate) and *apicalis* (pertaining to the apex), referring to the distinctive, feather-like branching pattern of the columella at the apex of the sporotheca.

Holotype: RUSSIA, Kamchatka Territory, Milkovsky District, vicinity of Lazo village, 55.4493° N, 159.7981° E, on a finally decayed log of *Betula platyphylla*, 18 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325372, GenBank *nrSSU*: PZ165591; *EF-1α*: PZ188784; *mtSSU*: PZ160600).

Diagnosis. Sporocarps measuring 3.4–3.9 mm in total height; stalk comprising 12%–43% of the total height; capillitium arises from the columella at nearly right angles in the middle of the sporotheca but shifts to an upward-pointing direction towards the apex; spores (6.6–)7.8–8.4(–8.9) μm in diameter, ornamented with simple reticulate with perforated muri, and pillars distinctly surpassing the muri tops.

Description: Sporocarps erect, stalked, densely to loosely gregarious, 3.4–3.9 mm in total height. Sporotheca cylindrical to tapering upwards, apex bluntly rounded, dark brown or lighter, 0.3–0.4 mm wide. Stalk black, shiny, (0.4–)0.6–1.2(–1.5) mm long, comprising 12%–43% of the total height, base forming a short cone. Hypothallus membranous, dark brown to deep brown, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex, not sinuous. Capillitium arising perpendicularly from the entire length of the columella, dense, dark brown to strong brown, with a triangular expansion at the point of origin; branching intricate, with membranous expansions frequently present at the branching nodes; threads nearly smooth, connecting to the surface net. Surface net well-developed, often incomplete at the sporotheca apex but complete elsewhere, with irregular polygonal meshes of unequal diameter, (4–)9–13(–26) μm; threads ornamented with irregularly distributed small warts, sparsely bearing spines. Spore concolorous with the sporotheca in mass, dark yellowish brown or lighter in transmitted light, globose to subglobose, (6.6–)7.8–8.4(–8.9) μm in diameter, ornamented with a simple reticulate type with perforated muri, characterized by pillars distinctly surpassing the tops of the muri, sparse and unequal meshes, meshes numbering about 7–9 across the spore diameter, and prominent perforations. Plasmodium not observed.

Additional materials examined: RUSSIA, Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.8635° N, 37.6464° E, on rotten wood, 22 Jul 2023, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 22874); Yaroslavl Region, Pereslavl-Zalessky Municipal District, Plesheevo Ozero National Park, 56.6979° N, 38.7939° E, on rotten bark of a coniferous tree, 9 Jul 2024, field, leg. Sakulin S.V. and Gmoshinskiy V.I. (MYX 24965).

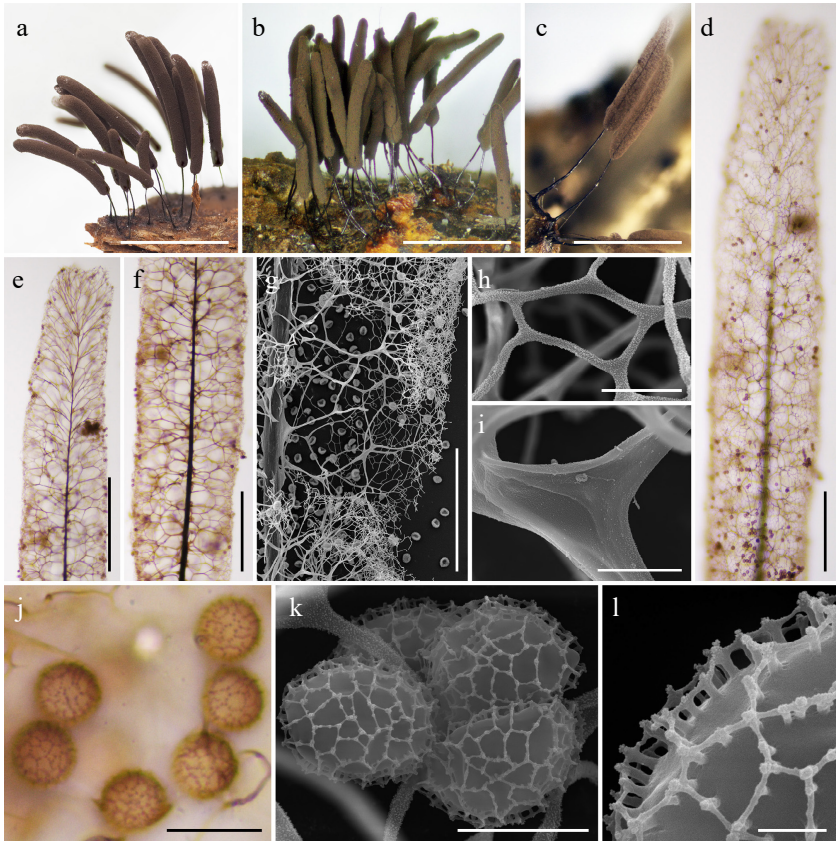

Fig. 27 Morphological characteristics of *Stemonitis pinnatiapicalis* (a) LE325372; (b), (d)–(g), (j), (l) MYX 24965; (c), (h), (i), (k) MYX 22874. (a)–(c) Mature sporocarps (DM). (d), (e) Apical region of the sporocarp (LM). (f) Capillitium in the middle part of the sporotheca (LM). (g) Capillitium in the middle part of the sporotheca (SEM). (h) Detail of the surface net (SEM). (i) Detail of the capillitium threads (SEM). (j) Spores (LM). (k) Spores (SEM). (l) Detail of the spore ornamentation (SEM). Scale bars: (a)–(c) = 2 mm; (d)–(g), (j) = 10 μm; (h), (i), (k) = 5 μm; (l) = 1 μm.

Distribution: currently known from European and Far Eastern Russia.

Habitat: on rotten wood.

Notes: Morphologically, *Ste. pinnatiapicalis* is most similar to *Ste. virginiensis*. The two species differ in several key morphological characteristics. The spore diameter of *Ste. virginiensis* is smaller (5–6.5 μm in the holotype; 5.6–8.2 μm in the syntype) and are described as having a broad reticulum with 3–5 meshes across the diameter and smooth, perforated muri[71,100]. In contrast, *Ste. pinnatiapicalis* has larger spores with a simple reticulate ornamentation in which the pillars distinctly exceed the muri tops (Fig. 27j–l). The columella of *Ste. virginiensis* is often curved or sinuous at the tip, whereas in *Ste. pinnatiapicalis* it is straight and tapers to the sporotheca apex (Fig. 27e). Furthermore, the surface net meshes of *Ste. virginiensis* are reported to be equal to or smaller than the spore diameter[71,100], while in *Ste. pinnatiapicalis* they are generally larger than the spore diameter. It should be noted that the identity of European material treated as *Ste. virginiensis* is uncertain; reported specimens are small-spored[18] but may not represent the true North American species. European records, including published illustrations, require careful re-examination. Based on these consistent differences in spore size, ornamentation type, columella morphology, and surface net mesh dimensions, *Ste. pinnatiapicalis* is clearly distinct from *Ste. virginiensis* and is here described as a new species. A direct molecular comparison was not possible, as the type of *Ste. virginiensis* and reliably identified fresh specimens from North America were unavailable for this study.

***Stemonitis pseudonigra* (G. Moreno, W.C. Rosing, D.W. Mitch. & S.L. Stephenson) Bortnikov & W.L. Song, comb. nov.**

MycoBank number: MB863330.

Basionym: *Comatricha pseudonigra* G. Moreno, W.C. Rosing, D.W. Mitch. & S.L. Stephenson, Bol. Soc. Micol. Madrid 31:172 (2007)

Notes: *Comatricha pseudonigra* was described from specimens obtained via moist chamber cultivation of bark collected in Australia[78]. It is characterized by its small sporotheca (0.15–0.2 mm in diameter), a long stalk with a fibrous base, sinuous capillitial threads, and small (5.5–6.5 μm), reticulate spores (see Moreno et al.[78]: figs 1–10). In the present study, it is transferred to *Stemonitis* as *Ste. pseudonigra*. This transfer is based primarily on its spore ornamentation, which is of the simple reticulate type with perforated muri, a defining characteristic of *Stemonitis* s.str. This interpretation is supported by the protologue, which notes that 'the ornamentation is similar to that observed in *Stemonitis fusca* and *Stemonaria longa*'; *Ste. fusca* is the type of *Stemonitis*, and the position of *Sta. longa* within *Stemonitis* has recently been confirmed[88].

The sporotheca of this species is globose to subglobose, differing from the typically cylindrical form of most *Stemonitis* species, and its capillitium is distinctly sinuous. These morphological deviations may further underscore that spore ornamentation holds greater taxonomic significance at the generic level than the shape of the sporotheca or the structure of the capillitial threads.

***Stemonitis reticulospora* (Ing & P.C. Holland) Bortnikov, W.L. Song, Novozh. & Shuang L. Chen, comb. nov.**

MycoBank number: MB863331.

Basionym: *Comatricha reticulospora* Ing & P.C. Holland, Trans. Brit. Mycol. Soc. 50 (4): 685 (1967).

Notes: *Comatricha reticulospora*, a rare European species, was described from East Sussex, England[94]. It is characterized by small sporocarps 2–2.5 mm in total height with a short stalk and a tangled capillitium without a surface net, which makes it very similar to other *Comatricha* species. However, its spores are (6–)8(–10) μm in diameter and warted-reticulate, which is the basis for its transfer to *Stemonitis* s.str. as *Ste. reticulospora*. It should be noted that the authors of the description also pointed out some similarity with *Ste. virginiensis* and species of *Stemonitopsis*[94].

Nevertheless, a modern study of the type specimen of this taxon, as well as fresh specimens from Europe, would be very useful for clarifying its morphology and phylogenetic position.

***Stemonitis rispaudii* (Hagelst.) Shchepin, Bortnikov, S.L. Stephenson, Schnittler & Novozh. Fig. 28**

MycoBank number: MB860496.

Synonyms: *Comatricha rispaudii* Hagelst., Mycologia 21 (5): 297 (1929).

Synonyms: *Paradiachea rispaudii* (Hagelst.) R.J.G. Hertel ex H. Neubert, Nowotny & K. Baumann, Die Myxomyceten Deutschlands und des angrenzenden Alpenraumes unter besonderer Berücksichtigung Österreichs, Band 3: Stemonitales: 250 (2000).

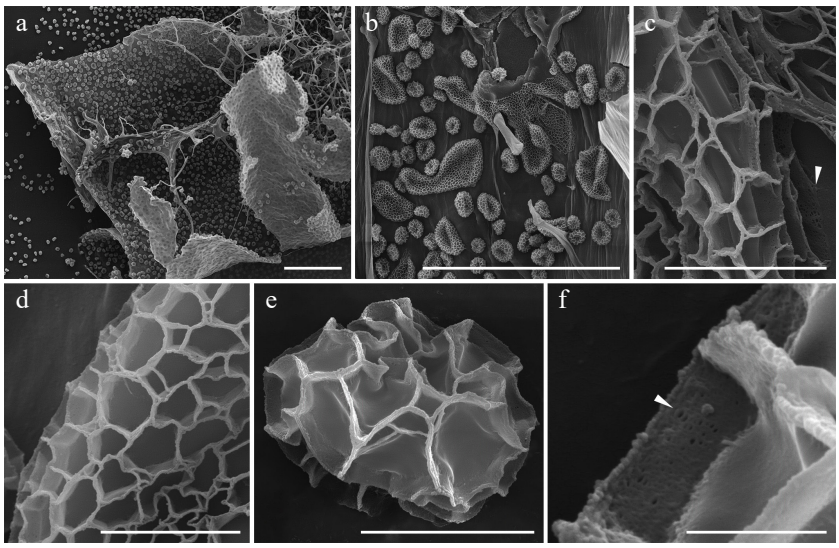

Fig. 28 Morphological characteristics of *Stemonitis rispaudii* (LE303142) under SEM. (a) Capillitium and peridium. (b)–(d) Flattened spore-like bodies and spores on the inner peridium surface. (e), (f) Spores. The punctiform perforations in the ridges of the spore ornamentation are shown by arrows (c, f). Scale bars: (a), (b) = 100 μm, (c), (d) = 5 μm, (f) = 1 μm.

Materials examined: VIETNAM, Lam Dong Province, Lac Duong District, Bidoup Nui Ba National Park, 12.1841° N, 108.6769° E, on leaf litter, 16 Nov 2014, field, leg. Novozhilov Yu.K. (LE303142).

Notes: *Stemonitis rispaudii* was originally described as *Com. rispaudii* from leaf litter in New York, USA. It was later revised to *P. rispaudii*[72] and recently transferred to *Stemonitis* s.str. based on the molecularly examined LE303142 specimen from Vietnam[88]. A recent study of the isosyntype of *Com. rispaudii*[98] has shown that this species is characterized by subsessile sporocarps on a restricted base, forming clusters of 7–10 sporocarps, 0.76–1.34 mm in total height and 0.34–0.46 in diameter. The peridium is retained on the lower third of the sporotheca and is often shared between adjacent sporocarps. The capillitium is fairly dense and does not form a surface net. Spores are violet-brown in mass, (8.6–)9.0–9.7(–10.3) μm in diameter, and banded-reticulate with 3–4(–5) meshes across the diameter; the ridges are low and occasionally have small perforations.

A repeated, detailed SEM examination of specimen LE303142 from a previous study by Shchepin et al.[88] shows that the spore muri are perforated by minute pores and that there are flattened spore-like bodies with reticulated ornamentation at the base of the sporangia, which confirms the species identification (Fig. 28d–f). The presence of small pore-like perforations in the spore muri (Fig. 28c, e, f; see Bortnikov et al.[98]: fig. 5g) confirms the placement of this species in *Stemonitis*.

***Stemonitis rossii* Ejale, Myxomycetes from south of Nigeria 179 (2010)**

MycoBank number: MB863443.

Notes: *Stemonitis rossii* was described from specimens collected from the bark of dead oil palm trees (*Elaeis guineensis*) in Opoji, Nigeria[117]. It is characterized by densely clustered sporocarps with sporotheca ca. 4.4 mm long, a stalk slightly longer than the sporotheca, and spores 7.0 μm in diameter bearing a verrucose-reticulate ornamentation. The protologue is brief and lacks illustrations. The species has rarely been reported since its description, but its spore ornamentation conforms to the circumscription of *Stemonitis* s.str.

***Stemonitis spinimuralis* W.L. Song & Shuang L. Chen, sp. nov. Fig. 29**

MycoBank number: MB863122.

Etymology: *spinimuralis* (Latin) with spiny walls, from *spina* (thorn, spine) and *muralis* (pertaining to a wall, of a wall), referring to the spore ornamentation, which features a simple reticulate type with perforated muri, where pillars distinctly surpass the tops of the muri.

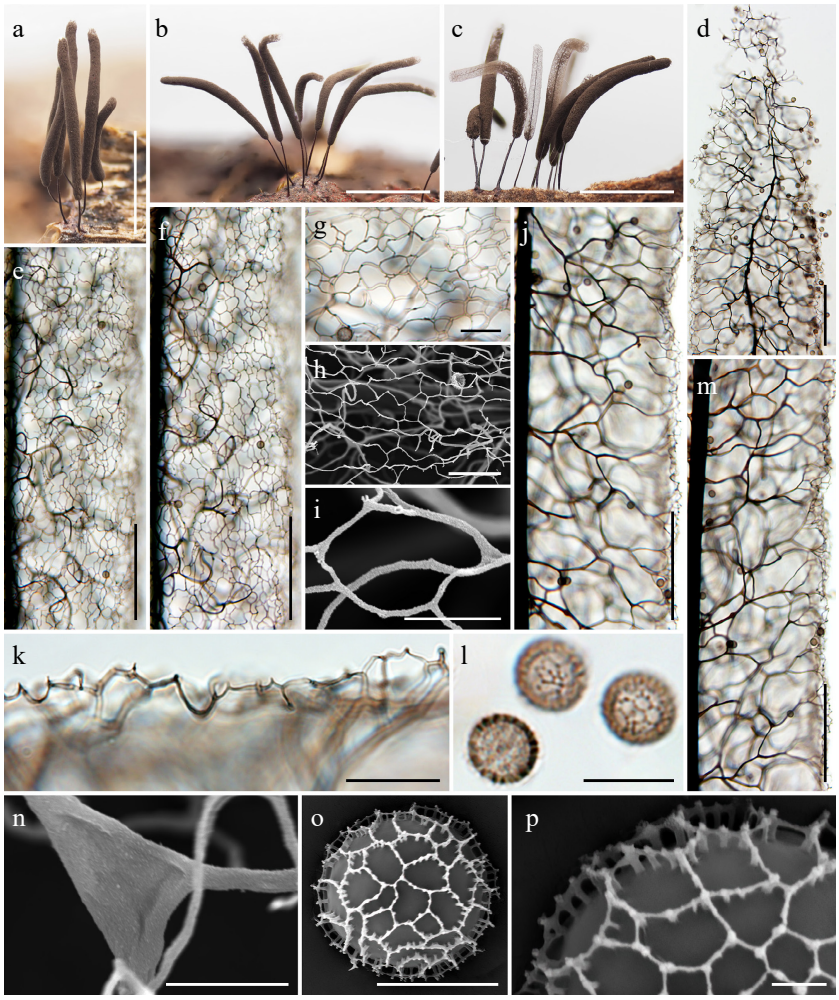

Fig. 29 Morphological characteristics of *Stemonitis spinimuralis* (a)–(m) HFNNU 2815; (n), (o) HMAS 0257700; (p) HFNNU 12498. (a)–(c) Mature sporocarps (DM). (d) Apical view of the sporotheca (LM). (e)–(g) Surface net (LM). (h), (i) Detail of the surface net (SEM). (j) Capillitium in the middle part of the sporotheca (LM). (k) Edge of the sporotheca (LM). (l) Spores (LM). (m) Capillitium in the middle part of the sporotheca (LM). (n) Detail of the capillitium threads (SEM). (o) Spore (SEM). (p) Detail of the spore ornamentation (SEM). Scale bars: (a)–(c) = 1 mm; (d)–(f), (j), (m) = 100 μm; (g), (h), (k) = 20 μm; (l) = 10 μm; (i), (n), (o) = 5 μm; (p) = 1 μm.

Holotype: CHINA, Henan Province, Nanyang City, Baotianman National Nature Reserve, 33.5244° N, 111.9695° E, on bark of a living tree, 27 Aug 2016, moist chamber, leg. Gao Y. and Wang G.W. (HFNNU 12496, GenBank *nrSSU*: PX940059; *mtSSU*: PX940079).

Diagnosis: Sporocarps measuring (2.1–)2.6–3.2(–3.6) mm in total height; stalk (0.4–)0.8–1.0(–1.3) mm (20%–40% of the total height); surface net with numerous capillitial spines of variable length; spore (7.5–)7.9–8.5(–9.3) μm in diameter, ornamentation a sparse, simple reticulum with perforated muri; pillars distinctly surpassing the tops of the muri, meshes numbering about 5–7 across the spore diameter.

Description: Sporocarps erect, stalked, loosely gregarious in small groups, (2.1–)2.6–3.2(–3.6) mm in total height. Sporotheca elongate-cylindrical, tapering towards both ends, apex bluntly rounded, dark brown, ca. 0.2 mm wide. Stalk black, shiny, (0.4–)0.8–1.0(–1.3) mm long, 20%–40% of the total height, base forming a short cone. Hypothallus membranous, dark grayish brown to deep brown, common to the colony, sometimes inconspicuous. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex, unbranched and filamentous at the apex. Capillitium arising nearly perpendicularly from the entire length of the columella, dark brown to moderate brown, with a triangular expansion at the point of origin, much and intricately branched; branching points with weak membranous expansions, often forming fusiform structures, threads nearly smooth or with minute warts, connecting to the surface net. Surface net well-developed, often incomplete at the sporotheca apex but complete elsewhere, threads slender and delicate; meshes of unequal diameter, (7–)12–18(–33) μm, threads bearing small warts and spines of variable length. Spore concolorous with the sporotheca in mass, brown or lighter in transmitted light, globose to subglobose, (7.5–)7.9–8.5(–9.3) μm in diameter, ornamented with a simple reticulate type with perforated muri, sometimes incomplete, characterized by sparse and unequal meshes, numbering about 5–7 across the spore diameter, pillars distinctly surpassing the tops of the muri, and prominent perforations. Plasmodium not observed.

Additional materials examined: CHINA, Henan Province, Nanyang City, Baotianman National Nature Reserve, 33.5244° N, 111.9695° E, on bark of a living tree, 27 Aug 2016, moist chamber, leg. Gao Y. and Wang G.W. (HFNNU 12498); Anhui Province, Luan City, Tiantangzhai National Forest Park, 31.6851° N, 115.8591° E, on litter, 23 May 2016, moist chamber, leg. Wang G.W. and Gao Y. (HMAS 0257700).

Distribution: currently known from Central and Eastern China.

Habitat: on litter and bark of a living tree.

Notes: *Stemonitis spinimuralis* is morphologically most similar to *Ste. nigrescens* (= *Ste. fusca*) and can be difficult to distinguish superficially. Detailed comparison with the holotype of *Ste. nigrescens*[100] reveals several consistent differences. The sporocarps of *Ste. spinimuralis* are dark grayish brown to brownish gray, whereas *Ste. nigrescens* is described as 'violet, not dark'. Its stalk is longer ([0.4–]0.8–1.0[–1.3] mm vs ca. 0.2 mm in *Ste. nigrescens)* and it possesses a well-developed surface net densely covered with spines of variable length, a characteristic not reported for *Ste. nigrescens*[100]. Furthermore, the spore reticulum of *Ste. spinimuralis* is relatively sparse (ca. 5–7 meshes across the diameter; Fig. 29l, o, p), unlike the dense reticulum of *Ste. nigrescens* (ca. 8–9 meshes across the diameter; see Castillo et al.[100]: figs 48, 49). These differences support the distinction of the two taxa. Comparison with the neotype of *Ste. fusca* (Ellis & Everhart's 2697)[100] also shows clear distinctions: the sporocarps of *Ste. spinimuralis* are much smaller, its stalk is shorter, and the surface net meshes ([7–]12–18[–33] μm) are distinctly larger than its spore diameter ([7.5–]7.9–8.5[–9.3] μm), whereas in the neotype the surface net meshes are similar in size to the spores.

Stemonitis spinimuralis also shows some similarity to *Ste. pinnati-apicalis* (Fig. 27) described in this study. However, the latter has larger sporocarps (3.4–3.9 mm in total height), a columella that tapers towards the sporotheca apex and gives rise to sparse capillitial branches (Fig. 27d), and a denser spore reticulum (ca. 7–9 meshes across the diameter; Fig. 27p). In contrast, *Ste. spinimuralis* has a columella that produces noticeably denser capillitial branches at the apex (Fig. 29e) and a sparser reticulum (Fig. 29l). Phylogenetically, the two species are distantly related (Fig. 1), confirming their morphological distinction.

***Stemonitis virginiensis* Rex, Proc. Acad. Nat. Sci. Philadelphia 43: 391 (1891)**

MycoBank number: MB224407.

Notes: *Stemonitis virginiensis* was described from the USA[92]. Its holotype was studied by Castillo et al.[100] and an isotype by Moreno et al.[71]. The species is characterized by small, rosy sporotheca and spores measuring 5–6.5 μm in diameter. The spores have a reticulum with very broad meshes; the muri are perforated and smooth on their upper surface (see Castillo et al.[100]: figs 53, 54; see Moreno et al.[71]: fig. 11d–f). This spore morphology is consistent with the circumscription of *Stemonitis* s.str.

• *Stemonitopsis* (Nann.-Bremek.) Nann.-Bremek., De Nederlandse Myxomyceten: 203 (1974)

MycoBank number: MB12237.

Type: *Stemonitopsis hyperopta* (Meyl.) Nann.-Bremek., De Nederlandse Myxomyceten: 206 (1975).

Emended diagnosis: Sporocarps stalked. Sporotheca cylindrical. Stalk usually shorter than the sporotheca. Peridium fugacious. Columella a continuation of the stalk, usually nearly reaching the apex. Capillitium arising evenly along the entire length of the columella, consisting of thread-like tubules, forming a three-dimensional internal net and an interrupted or fragmented surface net. Spores violet-brown to brown in mass, mostly smaller than 8(–9) μm, ornamented with numerous meshes of irregular sizes formed by delicate bands of low ridges.

Accepted species: *Stemonitopsis hyperopta* (Meyl.) Nann.-Bremek. sensu lato.

Morphospecies included in the genus but not yet phylogenetically studied: *Stemonitopsis meandrispora* (A. Castillo, G. Moreno & Illana) Bortnikov, Kireeva, Gmoshinskiy, W.L. Song & Novozh., *Stp. microspora* (Lister) Nann.-Bremek., *Stp. orthotricha* (Bratteng) Bortnikov, W.L. Song, Shuang L Chen & Novozh., *Stp. reticulata* (H.C. Gilbert) Nann.-Bremek. & Y. Yamam., and *Stp. subalpina* (M.L. Farr & S.L. Stephenson) Bortnikov, Gmoshinskiy & Novozh.

Temporarily formally recognized species: *Stemonitopsis aequalis* (Peck) Y. Yamam., *Stp. peritricha* (Nann.-Bremek.) Nann.-Bremek., and *Stp. subcaespitosa* (Peck) Nann.-Bremek.

Notes: Data from this study corroborate recent findings that *Stp. amoena* was transferred to *Stemonitis* s.str. and *Stemonitopsis typhina* (F.H. Wigg.) Nann.-Bremek. was designated as the type of the new genus *Argentoderma*[88] and confirm that the boundaries of *Stemonitopsis* should be restricted to species with relatively small reticulate spores bearing low ridges. Consequently, all *Stemonitopsis* species with warted spores require revision and reassessment of their generic classification.

The present study transfers *Stp. gracilis* to *Corallosporopsis* and *Stp. curiosa* to *Stemonitis* s.str. (see corresponding notes). Furthermore, based on morphological fit with the emended concept of *Stemonitopsis* and in accordance with Criterion B, this study

proposes the transfer of *Comatricha meandrispora* A. Castillo, G. Moreno & Illana., *Comatricha orthotricha* Bratteng, and *Comatricha subalpina* M.L. Farr & S.L. Stephenson to *Stemonitopsis* with new combinations.

Three species, *Stp. aequalis*, *Stp. peritricha*, and *Stp. subcaespitosa*, are retained in *Stemonitopsis* temporarily, as they lack both detailed morphological data from type material and molecular sequences, precluding a confident generic reassignment.

***Stemonitopsis hyperopta* (Meyl.) Nann.-Bremek., Nederlandse Myxomyceten (Zutphen) 206 (1975)**

MycoBank number: MB324056.

Materials examined: BELARUS, Minsk Region, Minsk District, Glebkovka Reserve, vicinity of Kolodishchi village, 53.9213° N, 27.7882° E, on rotten wood, 20 Aug 2023, field, leg. Moroz E.L. (MSK-F 43339); Vitebsk Region, Lyepyel District, Berezinsky Biosphere Reserve, vicinity of Domzharitsy village, 54.7538° N, 28.3061° E, on rotten wood, 21 Sep 2020, field, leg. Moroz E.L. (MSK-F 43581); Minsk Region, Myadzyel District, Narachanski National Park, vicinity of Yatsyny village, 54.9490° N, 26.4631° E, on rotten wood, 10 Sep 2024, field, leg. Moroz E.L. (MSK-F 43591). **CHINA**, Anhui Province, Luan City, Tiantangzhai National Forest Park, 31.7545° N, 116.4941° E, on rotten wood, 26 Jul 2015, field, leg. Wang G.W. and Gao Y. (HMAS 0258201, HMAS 0258202, HMAS 0258211); Henan Province, Xinyang City, Dasu Mountain National Forest Park, 114.2462° N, 31.9499° E, on rotten wood, 19 Oct 2022, field, leg. Lin D. (HMAS 0287307). **RUSSIA**, Krasnoyarsk Territory, Beryozovsky District, Stolby National Park, on decayed wood of *Betula pendula*, 13 Aug 2006, field, leg. Kosheleva A.P. (LE229360); Republic of Altai, Ongudaysky District, vicinity of Topuchaya village, 51.0964° N, 85.6264° E, on decayed wood of *Picea obovata*, 1 Aug 2008, field, leg. Novozhilov Yu.K. and Schnittler M. (LE254703); Karachayevo-Circassian Republic, Zelenchuksky District, 43.4858° N, 41.3153° E, on decayed wood of *Abies nordmaniana*, 21 Aug 2009, field, leg. Novozhilov Yu.K. (LE256628); Republic of Tatarstan, Zelenodolsky District, Volga-Kama Nature Reserve, 55.9094° N, 48.7719° E, on decayed wood, 24 Aug 2016, field, leg. Zemlyanskaya I.V. (LE279778); Karachayevo-Circassian Republic, Karachayevsky District, Teberda Nature Reserve, 43.4410° N, 41.7248° E, on decayed wood of *Abies nordmaniana*, 7 Jun 2012, field, leg. Novozhilov Yu.K., Schnittler M. and Erastova D.A. (LE289706); Karachayevo-Circassian Republic, Karachayevsky District, Teberda Nature Reserve, 43.3149° N, 41.6403° E, on decayed wood of *Abies nordmaniana*, 14 Aug 2012, field, leg. Novozhilov Yu.K., Erastova D.A. and Morozova Yu.A. (LE290805); Murmansk Region, Monchegorsk Municipal District, Laplandskiy State Nature Biosphere Reserve, 67.6660° N, 32.3661° E, on decayed wood of *Picea obovata*, 22 Aug 2015, field, leg. Novozhilov Yu.K., Shchepin O.N., Erastova D.A., and Tikhonova E.N. (LE306436); Murmansk Region, Kirovsk Municipal District, Polar-Alpine Botanical Garden-Institute, 67.6538° N, 33.6575° E, on decayed wood of *Picea obovata*, 23 Aug 2015, field, leg. Novozhilov Yu.K., Shchepin O.N., Erastova D.A., and Tikhonova E.N. (LE306482); Murmansk Region, Monchegorsk Municipal District, Laplandskiy State Nature Biosphere Reserve, 67.6673° N, 32.3730° E, on decayed wood of *Pinus sylvestris*, 28 Jul 2016, field, leg. Novozhilov Yu.K., Shchepin O.N., and Tikhonova E.N. (LE307638); Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.9165° N, 158.7151° E, on strongly decayed log of *Larix cajanderi*, 11 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325006); Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.8931° N, 158.6961° E, on strongly decayed log of *Larix cajanderi*, 13 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325108); Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.8985° N, 158.6966° E, on decayed log of *Salix* sp., 13 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325140); Amur Region, Zeysky District, Zeya Nature Reserve, 54.0789° N, 126.8920° E, on decayed wood of *Larix gmelinii*, 11 Sep 2024, field, leg. Bortnikov F.M. and Bortnikova N.A. (LE353076); Amur Region, Zeysky District, Zeya Nature Reserve, 54.0789° N, 126.8920° E, on decayed wood of *Larix gmelinii*, 11 Sep 2024, field, leg. Bortnikov F.M. and Bortnikova N.A. (LE353078); Novgorod Region, Kholmsky Municipal District, Rdeysky State Nature Reserve, 57.0650° N, 30.7346° E, on rotten wood, 19 Jul 2021, field, leg. Bortnikov F.M., Borzov N.I. and Gmoshinskiy V.I. (MYX 18542); Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.8638° N, 37.6310° E, on rotten wood, 22 Jul 2023, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 22831); Yaroslavl Region, Pereslavl-Zalessky Municipal District, Plesheevo Ozero National Park, 56.7264° N, 38.7594° E, on rotten wood, 17 Aug 2023, field, leg. Sakulin S.V. and Gmoshinskiy V.I. (MYX 24152); Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.8848° N, 37.6442° E, on rotten wood, 10 Jul 2024, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 24214).

Notes: *Stemonitopsis hyperopta*, the type species of *Stemonitopsis*, was described in 1919 as *Stemonitis hyperopta* Meyl.[118] and later transferred to *Stemonitopsis*[23]. It is characterized by caespitose, stalked sporocarps 2.5–5.0 mm in total height; a stalk 0.1–0.5 mm long (25%–50% of the total height); a columella that either gradually merges into the capillitium or ends abruptly at the sporotheca apex, often with a brownish expansion in the latter case; a capillitium rarely expanded; a delicate surface net with angular meshes 5–15 μm in diameter, the threads sometimes bearing small spines; and violet-brown to lilac-grey spores 5–7 μm in diameter, ornamented with a fine reticulum of small, fairly regular meshes[23]. The specimens identified here as *Stp. hyperopta* agg. form a monophyletic but heterogeneous phylogenetic group that evidently comprises several closely related species, including some of the *Stemonitopsis* spp. included here. Preliminary morphological analysis suggests some differences among potential subclades. However, a detailed revision of this genus is beyond the scope of the current study and is planned for future research.

***Stemonitopsis meandrispora* (A. Castillo, G. Moreno & Illana) Bortnikov, Kireeva, Gmoshinskiy, W.L. Song & Novozh., comb. nov.**

MycoBank number: MB863332.

Basionym: *Comatricha meandrispora* A. Castillo, G. Moreno & Illana., Mycotaxon 46:315 (1993).

Notes: *Comatricha meandrispora* is characterized by small sporocarps 1–1.5 mm in total height and small, incompletely banded-reticulate spores 5.5–7.0 μm in diameter with low, thin ridges[119]. It is morphologically very similar to and frequently confused with *Stp. hyperopta*, as both share cylindrical sporocarps, a fibrous stalk base, and subreticulate spores of comparable size[120]. However, *Com. meandrispora* can be distinguished by its smaller, darker sporocarps, shorter sporotheca, a columella that thins abruptly in the middle and is curved with a slight apical widening, less coarse capillitial filaments, and a spore reticulum composed of incomplete small ribs that sometimes form stellate or ring-shaped thickenings, unlike the more uniform low ribs of *Stp. hyperopta*[120].

Although the phylogenetic position of this species is not yet known, its placement in *Stemonitopsis* is considered to better reflect its morphological relationships with *Stp. hyperopta*, *Stp. microspora*, and *Stp. subalpina* (see below) than retention in *Comatricha*.

Therefore, this species is transferred to *Stemonitopsis* as *Stp. meandrispora*.

***Stemonitopsis microspora* (Lister) Nann.-Bremek., De Nederlandse Myxomyceten: 208 (1975)**

MycoBank number: MB324057.

Notes: *Stemonitopsis microspora* was proposed as a new combination based on *Stemonitis microspora* Lister[23], with the type locality in England[23]. The species is distinguished by its sporocarps, which are pale grey-violet when fresh, becoming brown with age; the sporotheca is 1.7–3.2 mm high and narrowly conical; spores are 3.5–4.5 μm in diameter, bearing a fine reticulum of low ridges, a combination of characteristics consistent with the emended diagnosis of *Stemonitopsis*. The species occurs predominantly on dead leaves, more rarely on dead wood or bark, a substrate preference that may provide an additional diagnostic characteristic for the genus. The taxonomic history of this species appears complex and warrants further study.

***Stemonitopsis orthotricha* (Bratteng) Bortnikov, W.L. Song, Shuang L Chen & Novozh., comb. nov.**

MycoBank number: MB863333.

Basionym: *Comatricha orthotricha* Bratteng, Mycologia 67(2):415 (1975).

Notes: *Comatricha orthotricha* has small sporocarps up to 1 mm in total height and minute spores (5.5–)6.5–9 μm in diameter, reticulate by bands 0.5 μm in height[121], aligning it with other species of *Stemonitopsis* with reticulate spores, as accepted in this study.

***Stemonitopsis reticulata* (H.C. Gilbert) Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 98: 325 (1995)**

MycoBank number: MB414197.

Notes: *Stemonitopsis reticulata* was proposed as a new combination[91] based on *Comatricha reticulata* H.C. Gilbert[108]. Spores of the type specimen measure 7–9 μm in diameter, while those of the specimens cited for the recombination (Y.Y. 13.298, NENB 16.902) are slightly larger, 9–10 μm. The protologue clearly illustrates a reticulum of variable mesh size[108], matching the emended diagnosis of *Stemonitopsis*. The taxonomic interpretation of this species may be complex and requires further investigation.

***Stemonitopsis subalpina* (M.L. Farr & S.L. Stephenson) Bortnikov, Gmoshinskiy & Novozh., comb. nov.**

MycoBank number: MB863334.

Basionym: *Comatricha subalpina* M.L. Farr & S.L. Stephenson, Mycotaxon 30:455 (1987).

Notes: *Comatricha subalpina* has small cylindrical sporocarps 1.0–1.5(–2.0) mm in height and small violet-brown spores 6–7 μm in diameter, banded-reticulate, with low and thin ridges, which brings this species closer to *Stp. hyperopta* (see Farr[122]: figs 9, 10). Given that the reticulate ornamentation is atypical for *Comatricha*, assigning this species to *Stemonitopsis* is taxonomically justified and highlights the need for further morphological and phylogenetic study.

• ***Symphytocarpus* Ing & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C 70 (2): 218 (1967)**

MycoBank number: MB12440.

Type: *Symphytocarpus flaccidus* (Lister) Ing & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C 70 (2): 217 (1967).

Emended diagnosis: Sporocarps gregarious or clustered, sometimes forming pseudoaethalia. Columella well developed, almost reaching the sporotheca apex. Capillitium arising from the entire length of the columella. Spores mostly rusty-brown in mass, ornamented with irregularly distributed, thick, short bacula; secondary ornamentation rough, finely verrucous or finely reticulate, rarely barely visible.

Accepted species: *Symphytocarpus dispersus* W.L. Song, Bortnikov, Shuang L. Chen & Novozh., *Sym. ferrugineus* (Ehrenb.) W.L. Song, Shuang-Lin Chen, Gmoshinskiy, Bortnikov & Novozh., *Sym. flaccidus* (Lister) Ing & Nann.-Bremek., *Sym. laxicarpicus* W.L. Song, Bortnikov, Gmoshinskiy, Shuang L. Chen & Novozh., *Sym. minor* Bortnikov, W.L. Song, Shuang L. Chen & Novozh., *Sym. pseudoflavogenitus* (A. Vlasenko & Novozh.) W.L. Song, Bortnikov, Gmoshinskiy, A. Vlasenko, Novozh. & Shuang L. Chen, *Sym. splendens* (Rostaf.) W.L. Song, Bortnikov, Gmoshinskiy, Shuang L. Chen & Novozh., *Sym. tenuipes* W.L. Song, Bortnikov, Novozh. & Shuang L. Chen, and *Sym. uniforatus* W.L. Song & Shuang L. Chen

Morphospecies included in the genus but not yet phylogenetically studied: *Symphytocarpus microsporus* (Nann.-Bremek. & Y. Yamam.) W.L. Song, Bortnikov, Gmoshinskiy, Shuang-Lin Chen & Novozh., *Sym. planus* (B. Zhang & Yu Li) Bortnikov, W.L. Song & Novozh., *Sym. rhizoideipes* (Nann.-Bremek., R. Sharma & K.S. Thind) W.L. Song, Bortnikov, Gmoshinskiy &, A. Vlasenko, *Sym. rubescens* (Y. Yamam.) W.L. Song, Bortnikov, Gmoshinskiy, Novozh., & Shuang L. Chen, and *Sym. sichuanensis* (B. Zhang & Yu Li) Bortnikov, W.L. Song & Novozh.

Temporarily formally recognized species: *Symphytocarpus confluens* (Cooke & Ellis) Ing & Nann.-Bremek., *Sym. cristatus* Nann.-Bremek., *Sym. herbaticus* Ing, *Sym. impexus* Ing & Nann.-Bremek., and *Sym. syncarpus* (Yamash.) Y. Yamam.

Notes: Prior to this study, eight species were accepted in *Symphytocarpus*[6], a genus historically diagnosed by its pseudoaethalial habit (sessile, crowded sporocarps), a tubular, longitudinally striate columella (rarely absent), often persistent peridial flakes, a capillitium forming only an internal net or very sparse branches, and dark brown, ferruginous, purplish-brown, or sooty-black spores in mass. Recently, *Sym. amaurochaetoides* was transferred to *Stemonitis*[88].

Phylogenetic analysis conducted in this study (Fig. 1) indicates that *Sym. macrosporus* should be transferred to *Amaurochaete* (see corresponding notes). The clade containing the type species, *Sym. flaccidus*, defines the emended *Symphytocarpus*. Members of this clade possess gregarious to clustered sporocarps (sometimes pseudoaethalial), a well-developed columella, and rusty-brown spores in mass ornamented with irregularly distributed, thick, short bacula; a secondary ornamentation (finely verrucose to reticulate, sometimes inconspicuous) is also present. Based on morphological and/or phylogenetic evidence, this study transfers the following taxa to *Symphytocarpus* with new combinations: *Stemonitis aequalis* var. *microspora* Nann.-Bremek. & Y. Yamam. (elevated to species rank), *Stemonitis pallida* var. *rubescens* Y. Yamam. (elevated to species rank), *Ste. plana*, *Ste. pseudoflavogenita*, *Ste. rhizoideipes*, and *Ste. sichuanensis*.

Several specimens (LE325220, LE285115, MYX 25012, MSK-F 43596) align morphologically with the emended diagnosis but are not formally described here due to insufficient evidence. The newly described *Sym. dispersus*, although morphologically consistent with *Symphytocarpus*, falls outside the core phylogenetic clade; it is provisionally retained in the genus (see corresponding notes), rendering *Symphytocarpus* paraphyletic in the present analysis; a pattern that may be clarified by future study with additional material.

Five previously accepted species of *Symphytocarpus* (*Sym. confluens*, *Sym. cristatus*, *Sym. herbaticus*, *Sym. impexus*, *Sym. syncarpus*) currently lack molecular data. While some have been subject to morphological study, the available data (e.g., from types or authenticated specimens) are either insufficient in resolution or too limited

(see Moreno et al.[71]: fig. 16 for *Sym. herbaticus*; see Salamaga et al.[123] for *Sym. cristatus*) to allow reliable generic placement. Therefore, taxonomic changes for these taxa are deferred pending further investigation.

***Symphytocarpus dispersus* W.L. Song, Bortnikov, Shuang L. Chen & Novozh., sp. nov. Fig. 30**

MycoBank number: MB863231.

Etymology: *dispersus* (Latin) dispersed, scattered; from *dispersus*, past participle of *dispergere* (to scatter, disperse), referring to the growth habit of the sporocarps, which typically occur in sparse, widely scattered clumps, rather than in dense aggregations.

Holotype: RUSSIA, Primorye Territory, Khasansky District, Kedrovaya Pad Nature Reserve, 43.1131° N, 131.5160° E, on decayed deciduous wood, 19 Jul 2016, field, leg. Bortnikov F.M. (LE352558, GenBank *nrSSU*: PZ165601; *EF-1α*: PZ188793).

Diagnosis: Sporocarps scattered, mostly 2.3–3.6 mm in total height; stalk 30%–40% of total height, noticeably thick, 40–80 μm wide; capillitium very dense; surface net irregular and wavy, not flat; spores about 5.5–6.0 μm in diameter, finely warted under LM, finely spinulose under SEM.

Description: Sporocarps erect, stalked, loosely gregarious to scattered, (1.8–)2.4–3.2(–3.9) mm in total height. Sporotheca cylindrical to shortly cylindrical, often arcuate, tapering towards both ends, apex bluntly rounded, strong brown to deep orange-brown, 0.2–0.4 mm wide. Stalk black, robust, 40–80 μm wide, shiny, (0.5–)0.8–1.1 mm long, (22%–)27%–46% of the total height, base forming a short cone. Hypothallus membranous, black to deep brown, common to the colony. Peridium evanescent. Columella black, tapering upwards but not filamentous, reaching the sporotheca apex, unbranched. Capillitium arising densely from the entire length of the columella, deep brown to brownish orange, with a triangular expansion at the point of origin, lines dense, sinuous, highly and intricately branched, with membranous expansions at the branching points (sometimes inconspicuous), threads nearly smooth, connecting to the surface net or forming some free ends. Surface net poorly developed, incomplete to irregular, not in the same plane, making it difficult to observe under LM, lacking or rarely with spines, meshes irregularly polygonal, of unequal diameter, (6–)13–28(–49) μm, threads nearly smooth. Spore concolorous with the sporotheca in mass, pale brown or lighter in transmitted light, globose to subglobose, (4.8–)5.5–5.9(–6.5) μm in diameter, ornamented with sparsely distributed bacula, sometimes appearing echinate, secondary ornamentation variable, finely verrucous to finely reticulate. Plasmodium not observed.

Additional materials examined: CHINA, Anhui Province, Luan City, Tiantangzhai National Forest Park, 31.7545° N, 116.4941° E, on rotten wood, 26 Jul 2015, field, leg. Wang G.W. and Gao Y. (HMAS 0258207, HMAS 0258208, HMAS 0258209, HMAS 0258217); Henan Province, Nanyang City, Baotianman National Nature Reserve,

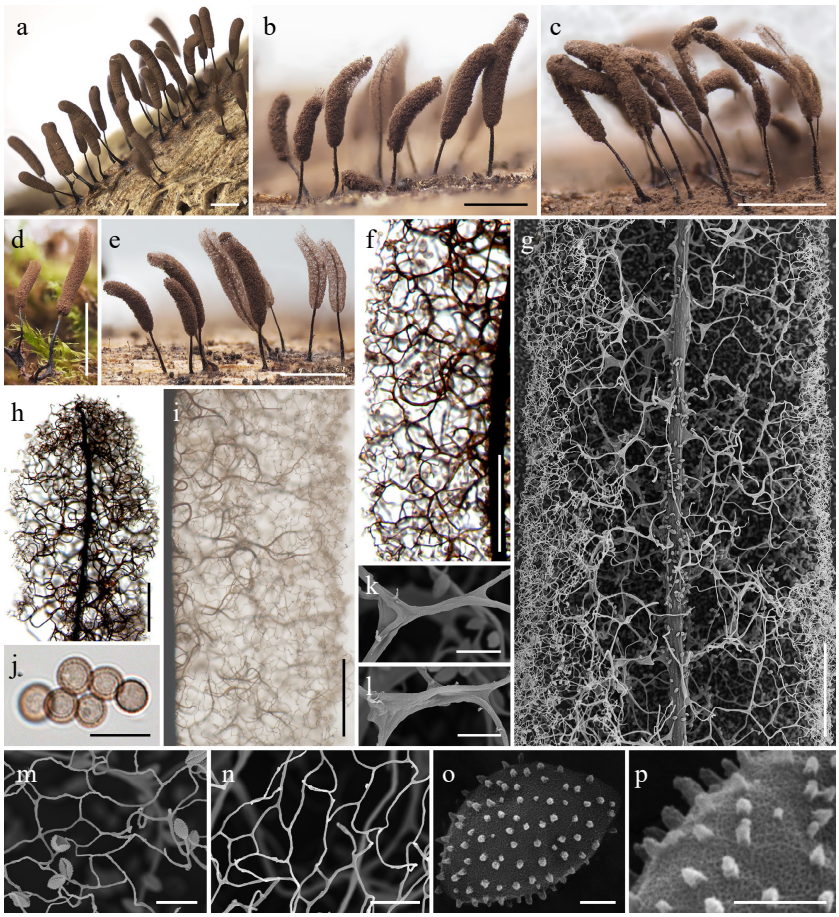

Fig. 30 Morphological characteristics of *Symphytocarpus dispersus* (a) LE327886; (b), (e), (f) HMAS 0258209; (c) HMAS 0258208; (g), (k)–(n) LE348844; (h), (j) HMAS 0258217; (d), (i), (o), (p) LE352558. (a)–(e) Mature sporocarps (DM). (f) Capillitium in the middle part of the sporotheca (LM). (g) Capillitium in the middle part of the sporotheca (SEM). (h) Apical region of the sporotheca (LM). (i) Surface net (LM). (j) Spores (LM). (k), (l) Detail of the capillitium threads (SEM). (m), (n) Detail of the surface net (SEM). (o) Spore (SEM). (p) Detail of spore ornamentation (SEM). Scale bars: (a)–(e) = 1 mm; (f)–(i) = 100 μm; (j)–(n) = 10 μm; (o), (p) = 1 μm.

33.0502° N, 111.8385° E, on rotten wood, 28 Jul 2015, field, leg. Gao Y. and Wang G.W. (HMAS 0258258). **RUSSIA**, Primorye Territory, Khasansky District, Kedrovaya Pad Nature Reserve, 43.1681° N, 131.4811° E, on decayed deciduous wood, 10 Jul 2020, field, leg. Bortnikova N.A. (LE327886); Primorye Territory, Khasansky District, Kedrovaya Pad Nature Reserve, 43.1362° N, 131.4996° E, on decayed coniferous wood, 24 Jul 2020, field, leg. Bortnikova N.A. (LE328106); Jewish Autonomous Region, Obluchensky District, Bastak Nature Reserve, 49.0950° N, 133.0662° E, on decayed coniferous moss-covered wood, 2 Jul 2022, field, leg. Bortnikova N.A. (LE348844).

Distribution: currently known from Central and Eastern China and Far Eastern Russia.

Habitat: on rotten wood.

Notes: Phylogenetically, *Sym. dispersus* is the sister taxon to *Stp. hyperopta* agg. (the type species of *Stemonitopsis*) (UBS/PP/TBE = 82/-/-, Fig. 1). However, the spores of *Sym. dispersus* exhibit the secondary ornamentation (Fig. 30p) typical for *Symphytocarpus*, and this new species is therefore described as a member of *Symphytocarpus* (See the criteria in the section Taxonomic framework and delimitation criteria), further investigations with more available material might change this pattern.

Symphytocarpus dispersus resembles *Ste. aequalis* var. *microspora*[99] considered here as *Sym. microsporus* (see below). Both species have a similar sporocarp habit, including a noticeably thick stalk, a dense capillitium with an incomplete surface network, and relatively small, warted spores. Detailed examination of the holotype of *Sym. microsporus* (TNS-M-Y-22052 = YY-626), however, reveals stable differences: its sporocarps are larger (4–5 mm vs 2.3–3.6 mm), its capillitium is less dense and simply branched, and its spores are slightly smaller (mostly 4.5–5.0 vs 5.5–6.0 μm).

The smallest sporocarps of *Sym. dispersus*, up to 2 mm in size (which, however, are usually found alongside larger ones in the same colony), can be confused with *Stp. gracilis*, considered here as *Cor. gracilis*, since this species also has small spores 5–7 μm in diameter[23]. The most distinctive characteristic allowing these species to be distinguished without the use of SEM (to reveal details of spore ornamentation) is the relative length of the stalk: about 20% in *Cor. gracilis* and 30%–40% in *Sym. dispersus*.

***Symphytocarpus ferrugineus* (Ehrenb.) W.L. Song, Shuang-Lin Chen, Gmoshinskiy, Bortnikov & Novozh., comb. nov. Figs 31–34**

MycoBank number: MB863335.

Basionym: *Stemonitis ferruginea* Ehrenb., Sylvae mycologicae Berolinenses: 25 (1818).

Synonyms: *Stemonitis axifera* (Bull.) T. Macbr., North American Slime Moulds: 120 (1889).

Materials examined: BELARUS, Minsk City, Pyershamayski District, Central Botanical Garden of NAS of Belarus, 53.9165° N, 27.6114° E, on rotten wood, 6 Sep 2018, field, leg. Moroz E.L. (MSK-F 41151-1); Minsk Region, Myadzyel District, Narachanski National Park, vicinity of Yatsyny village, 54.9510° N, 26.4716° E, on rotten wood, 10 Sep 2024, field, leg. Moroz E.L. (MSK-F 43508); Minsk Region, Myadzyel District, Narachanski National Park, vicinity of Alsheva village, 54.9610° N, 26.3742° E, on rotten wood, 14 Jul 2018, field, leg. Moroz E.L. (MSK-F 43579). **CHINA**, Heilongjiang Province, Greater Khingan Range Prefecture, Guqigu National Wetland Park, on rotten wood, 28 Jul 2024, field, leg. Chen S.L. and Yan S.Z. (HFNNU 11577); Heilongjiang Province, Greater Khingan Range Prefecture, Mengke Mountain Forest Farm of Tahe Forestry Bureau, on rotten wood, 29 Jul 2024, field, leg. Chen S.L. and Yan S.Z. (HFNNU 11586, HFNNU 11590); Xinjiang Uygur Autonomous Region, Altay Prefecture, Jiadengyu National Forest Park, 48.5722° N, 87.0913° E, on rotten wood, 2 Aug 2022, field, leg. Chen S.L. (HFNNU 12499); Gansu Province, Diebu County, Luoda Forest Farm, 34.0500° N, 103.1400° E, on dead bark, 31 Jul 1998, field, leg. Chen S.L. (HMAS

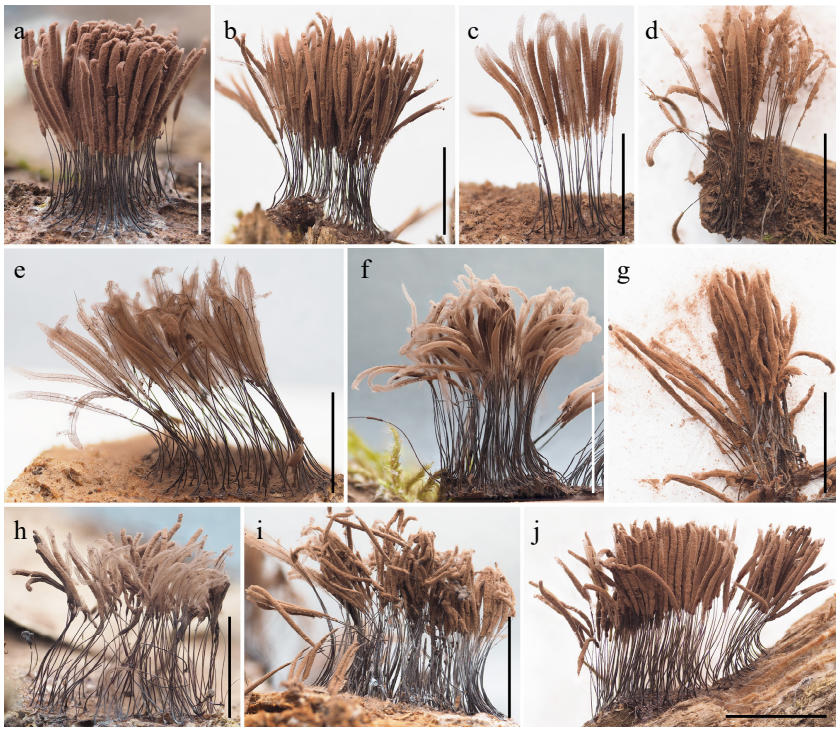

Fig. 31 Mature sporocarps of *Symphytocarpus ferrugineus* (DM). (a) Specimen HFNNU 11590. (b) Specimen HFNNU 11586. (c) Specimen MSK-F 43579. (d) Specimen LE328196. (e) Specimen MSK-F 41151-1. (f) Specimen MSK-F 43508. (g) Specimen LE259805. (h) Specimen HFNNU 12499. (i) Specimen HMAS 75392. (j) Specimen HFNNU 11577. Scale bars: 2 mm.

https://doi.org/10.48130/mycosphere-0026-0012

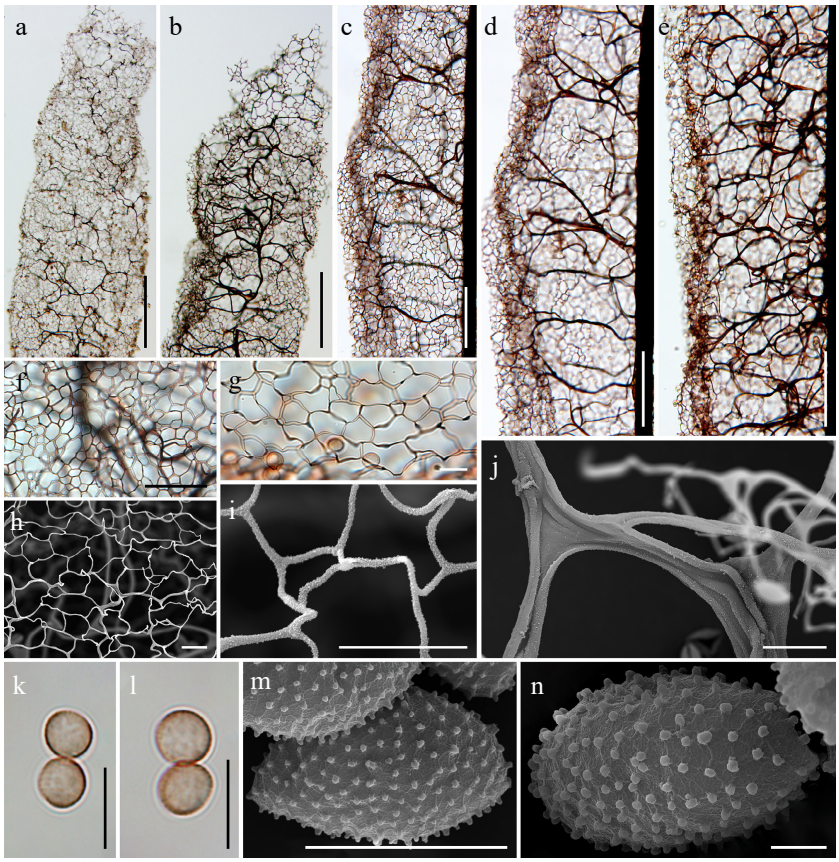

Fig. 32 Morphological characteristics of *Symphytocarpus ferrugineus* (a) HFNNU 11590; (b) HFNNU 11586; (c), (k), (l) LE320987; (d) LE328196; (e) MSK-F 41151-1; (f) MSK-F 43508; (g) LE259805; (h) HFNNU 12499; (i) HMAS 75392; (j) HFNNU 11577; (m) MYX 19217; (n) MYX 24329. (a), (b) Apical region of the sporotheca (LM). (c) Surface net (LM). (d), (e) Capillitium in the middle part of the sporotheca (LM). (f), (g) Detail of the surface net (LM). (h), (i) Detail of the surface net (SEM). (j) Detail of the capillitium threads (SEM). (k), (l) Spores (LM). (m), (n) Spore (SEM). Scale bars: (a), (b) = 200 μm; (c)–(e) = 100 μm; (f) = 50 μm; (g)–(l) = 10 μm; (m) = 5 μm; (n) = 1 μm.

75392). **RUSSIA**, Altai Territory, Barnaul Urban District, South-Siberian Botanical Garden, 53.2653° N, 83.6745° E, on decayed wood of *Betula pendula*, 29 Jul 2008, field, leg. Vlasenko A.V. (LE254641); Altai Territory, Talmensky District, vicinity of Ozerki village, 53.8244° N, 83.7739° E, on leaf litter, 25 Jun 2008, field, leg. Vlasenko A.V. (LE259801); Altai Territory, Pervomaysky District, vicinity of Losikha village, 53.3217° N, 84.0764° E, on litter of pine needles, 23 Jun 2008, field, leg. Vlasenko A.V. (LE259805); Primorye Territory, Khasansky District, Kedrovaya Pad Nature Reserve, 43.1419° N, 131.4945° E, on decayed deciduous wood, 24 Jul 2020, field, leg. Bortnikova N.A. (LE328110); Primorye Territory, Khasansky District, Kedrovaya Pad Nature Reserve, 43.1407° N, 131.4554° E, on decayed deciduous wood, 11 Jul 2020, field, leg. Bortnikova N.A. (LE328196); Vladimir Region, Sudogodsky District, vicinity of Lobanovo village, 56.0090° N, 40.8130° E, on rotten wood, 21 Jun 2021, field, leg. Mishulin A.A. and Gmoshinskiy V.I. (MYX 19217); Vladimir Region, Sudogodsky District, vicinity of Lobanovo village, 56.0166° N, 40.8122° E, on leaf litter of deciduous trees, 10 Nov 2021, field, leg. Mishulin A.A. and Gmoshinskiy V.I. (MYX 19508); Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.8867° N, 37.6352° E, on rotten wood, 06 Jul 2022, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 20665); Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.8635° N, 37.6464° E, on rotten wood, 11 Jul 2024, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 24269); Yaroslavl Region, Pereslavl-Zalessky, Plesheevo Ozero National Park, 56.8185° N, 38.7698° E, on rotten wood, covered by moss, 19 Jun 2024, field, leg. Sakulin S.V. and Gmoshinskiy V.I. (MYX 24329). **UNITED STATES OF AMERICA**, Arkansas, Washington County, 35.7796° N, 94.2486 W, on decayed deciduous wood, 20 Aug 2005, field, leg. Novozhilov Yu.K. and Rollins A. (LE245001).

Notes: *Stemonitis ferruginea* was first described from Germany[124]. The name *Ste. axifera* (Bull.) T. Macbr., however, has taxonomic priority, as it is based on the earlier basionym *Trichia axifera* Bull. (1790) with the combination published in 1889. Consequently, most subsequent taxonomic treatments regarded *Ste. ferruginea* as a later synonym of *Ste. axifera*[6,13,23,72,76,83,125–128]. A critical issue is that the original material of *T. axifera* is not extant, making the application of the name *Ste. axifera* ambiguous. For this reason, Moreno et al.[71] after examining the type specimen of *Ste. ferruginea* and reviewing of the literature, proposed to treat the widely cited name '*Ste. axifera* auct.' as a *nomen ambiguum*. They argued for the reinstatement of *Ste. ferruginea* as an independent species, reviving the interpretation of Lister[97], and recommended treating '*Ste. axifera* auct.' as a synonym of *Ste. ferruginea*.

The morphological characteristics of the specimens examined here align closely with the revised description of *Ste. ferruginea* provided by Moreno et al.[71]. A key characteristic is the spore ornamentation, which consists of scarce, thick, short bacula that are irregularly distributed and overlaid by a dense, delicate reticulum (Fig. 32m, n). However, in specimen LE254641, the bacula are notably denser (Fig. 34k, l). The sporocarps show some variation in total height, stalk length, and sporotheca width, although all retain a gregarious habit (Fig. 31). The surface net threads are mostly filamentous and bear a few small spines (Fig. 31c, f–i), matching the supplementary description of Moreno et al.[71]. However, in

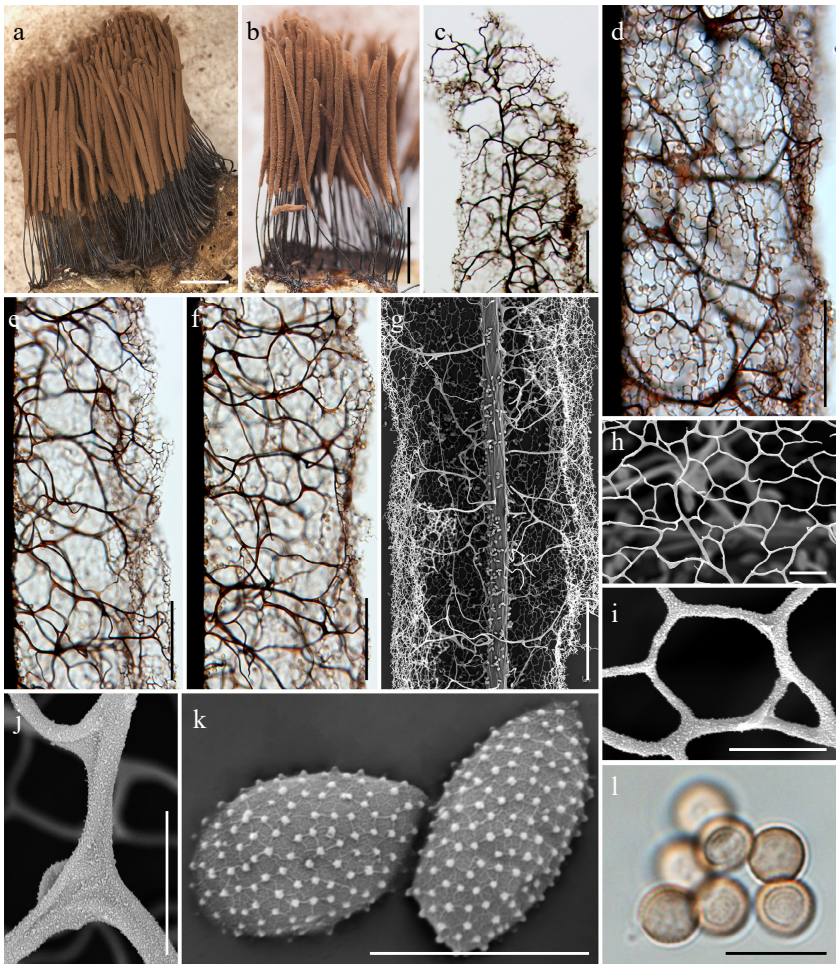

Fig. 33 Morphological characteristics of *Symphytocarpus ferrugineus* (LE245001, USA). (a), (b) Mature sporocarps (DM). (c) Apical region of the sporotheca (LM). (d) Surface net (LM). (e), (f) Capillitium in the middle part of the sporotheca (LM). (g) Capillitium in the middle part of the sporotheca (SEM). (h), (i) Detail of the surface net (SEM). (j) Detail of the capillitium threads (SEM). (k) Spores (SEM). (l) Spores (LM). Scale bars: (a), (b) = 2 mm; (c)–(g) = 100 μm; (h), (l) = 10 μm; (i)–(k) = 5 μm.

specimens LE254641 (Fig. 34f, g) and LE245001 (Fig. 33d, h, i), the threads are distinctly flattened and ribbon-like, contrasting with the filamentous form observed in most other specimens; the mesh diameter and thread ornamentation, however, remain similar.

Phylogenetic analysis revealed that LE254641 and LE245001 exhibit sequence divergence from the majority of other *Ste. ferruginea* specimens, forming three distinct but monophyletic branches (UBS/PP/TBE = 100/100/100; Fig. 1). Given their high morphological similarity and the presence of intermediate forms, it is considered premature to describe LE254641 and LE245001 as separate species. Future expanded sampling is needed to verify whether surface net thread morphology and spore ornamentation density are reliable diagnostic characteristics. The molecular divergence of LE245001 (from the USA) may reflect geographical isolation. Notably, despite this intraspecific variation, all branches identified as *Ste. ferruginea* form a strongly supported clade in the three-gene phylogeny (UBS/PP/TBE = 100/100/100; Fig. 1), robustly supporting its recognition as an independent species. *Stemonitis ferruginea* is phylogenetically closely related to the clade containing *Sym. flaccidus*, the type of *Symphytocarpus* (Fig. 1). Its morphology, densely gregarious sporocarps with brown sporotheca and spores ornamented with bacula bearing a distinct, delicate reticulum, fits the emended circumscription of *Symphytocarpus*. Therefore, based on the combination of morphological and phylogenetic evidence, *Ste. ferruginea* is formally reinstated and transferred to *Symphytocarpus* as *Sym. ferrugineus*.

***Symphytocarpus flaccidus* (Lister) Ing & Nann.-Bremek., Proc. Kon. Ned. Akad. Wetensch., C. 70(2):217 (1967)**

MycoBank number: MB339893.

Materials examined: BELARUS, Brest Region, Kamyenyets District, Belovezhskaya Pushcha National Park, vicinity of Kamenyuki village, 52.5998° N, 23.8106° E, on rotten wood, 10 Jun 2020, field, leg. Moroz E.L. (MSK-F 43587). **RUSSIA**, Republic of Karelia, Loukhsky District, The White Sea, Sredny Island, 66.2922° N, 33.6611° E, on decayed wood, 19 Jul 1993, field, leg. Novozhilov Yu.K. (LE47610); Republic of Karelia, Loukhsky District, The White Sea, Sredny Island, 66.2922° N, 33.6611° E, on decayed wood, 19 Jul 1993, field, leg. Novozhilov Yu.K. (LE47624); Altai Territory, Pervomaysky District, vicinity of Losikha village, 53.3447° N, 84.1228° E, on decayed log of *Pinus sylvestris*, 8 Jul 2009, field, leg. Vlasenko A.V. (LE266132); Moscow Region, Odintsovo Urban District, vicinity of Skadovsky Zvenigorod Biological Station, 55.6994° N, 36.7322° E, on decayed log of *Betula pendula*, 1 Aug 2017, field, leg. Zemlyanskaya I.V. (LE279585); Murmansk Region, Monchegorsk Municipal District, Laplandskiy State Nature Biosphere Reserve, 67.6512° N, 32.6509° E, on decayed wood of *Picea obovata*, 18 Aug 2015, field, leg. Novozhilov Yu.K., Shchepin O.N., Erastova D.A., and Tikhonova E.N.

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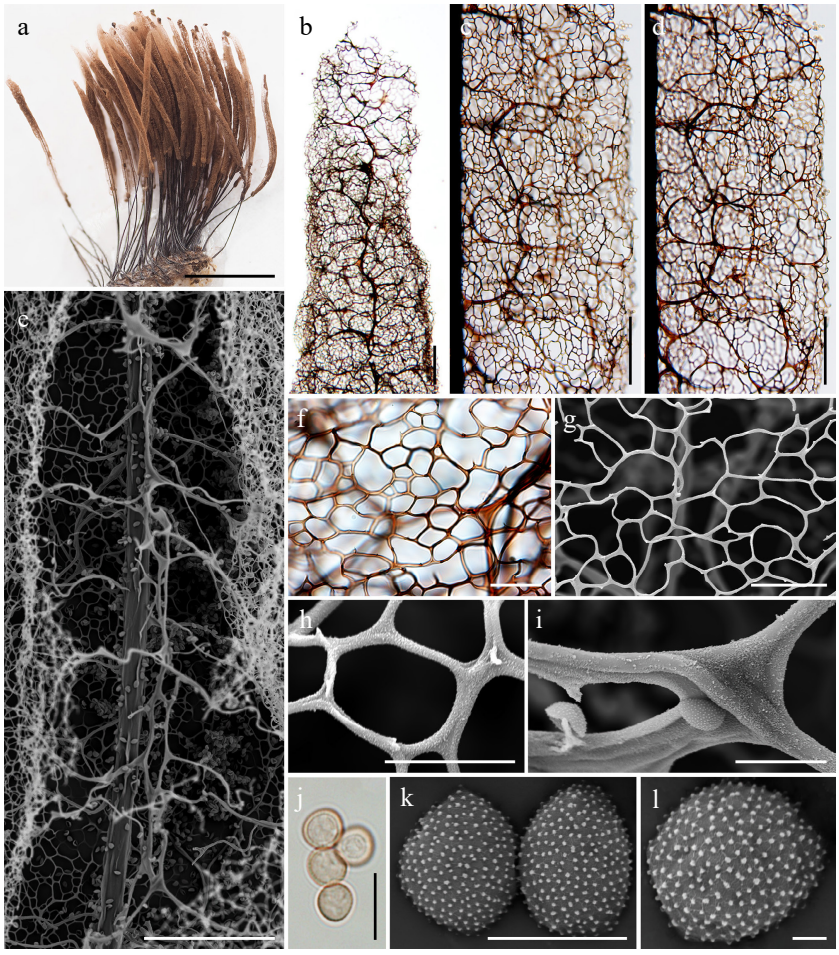

Fig. 34 Morphological characteristics of *Symphytocarpus ferrugineus* (LE254641). (a) Mature sporocarps (DM). (b) Apical region of the sporotheca (LM). (c) Surface net (LM). (d) Capillitium in the middle part of the sporotheca (LM). (e) Capillitium in the middle part of the sporotheca (SEM). (f) Detail of the surface net (LM). (g), (h) Detail of the surface net (SEM). (i) Detail of the capillitium threads (SEM). (j) Spores (LM). (k), (l) Spores (SEM). Scale bars: (a) = 1.5 mm; (b)–(e) = 100 μm; (f), (g) = 20 μm; (h)–(j) = 10 μm; (k)= 5 μm; (l)= 1 μm.

(LE306034); Murmansk Region, Monchegorsk Municipal District, Laplandskiy State Nature Biosphere Reserve, 67.6512° N, 32.6509° E, on decayed wood of *Picea obovata*, 18 Aug 2015, field, leg. Novozhilov Yu.K., Shchepin O.N., Erastova D.A., and Tikhonova E.N. (LE306037); Karachayevo-Circassian Republic, Karachayevsky District, Teberda Nature Reserve, 43.4438° N, 41.7300° E, on decayed wood of *Pinus sylvestris*, 8 Jul 2019, field, leg. Novozhilov Yu.K., Gmoshinskiy V.I., Shchepin O.N., Prikhodko I.S., Zemlyanskaya I.V. and Matveev A.V. (LE324698); Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.8931° N, 158.6961° E, on slightly decayed log of *Larix cajanderi*, 13 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325101); Pskov Region, Bezhanitsky Municipal district, Polystovskiy State Nature Reserve, 57.0985° N, 30.3743° E, on rotten wood, 31 Jul 2020, field, leg. Gmoshinskiy V.I. and Borzov N.I. (MYX 16194); Moscow Region, Serpukhovsky District, Prioksko-Terrasny Nature Biosphere Reserve, 54.9132° N, 37.5935° E, on dead fragments of the bark of a living tree, 9 May 2025, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 25026).

Notes: *Symphytocarpus flaccidus*, originally described as *Stemonitis splendens* var. *flaccida*[97], was established as the type of *Symphytocarpus*[22]. The lectotype (BM 1376) was designated by Lado & Wrigley de Basanta[129] based on its matching locality, date, and collector with the material cited by Lister[97]; no images were provided. This designation supersedes the earlier lectotype (BM 1377) proposed by Ing & Nannenga-Bremekamp[22]. Moreno et al.[71] examined BM 1377 and provided SEM images of its spores, but the resolution was insufficient to confirm the presence or absence of secondary ornamentation.

In the present study, some specimens match the morphological description of *Sym. flaccidus* by Moreno et al.[71] and are accordingly identified. This clade forms a well-supported sister group to *Sym. pseudoflavogenitus* (UBS/PP/TBE = 100/-/-; Fig. 1). Other specimens (LE279585, LE325101, and MYX 16194) are treated conservatively as *Sym.* aff. *flaccidus* due to inconclusive evidence; these form a distinct, well-supported clade sister to *Sym. splendens* (UBS/PP/TBE = 100/100/100; Fig. 1). Although the two flaccidus-related clades are not sisters, both nest within the larger *Symphytocarpus* lineage, consistent with the current generic placement. Their status may be resolved with broader sampling.

***Symphytocarpus laxicarpicus* W.L. Song, Bortnikov, Gmoshinskiy, Shuang L. Chen & Novozh., sp. nov. Fig. 35**

MycoBank number: MB863124.

Etymology: *laxicarpicus* (Latin) with loose or slack sporocarps, from *laxus* (loose, slack, open) and *carpicus* (pertaining to fruit or fruiting bodies), referring to the loosely and sparsely arranged sporocarps, in contrast to the densely clustered habit typical of many related species.

Holotype: RUSSIA, Jewish Autonomous Region, Obluchensky District, Bastak Nature Reserve, 49.0691° N, 133.0739° E, on decayed

Fig. 35 Morphological characteristics of *Symphytocarpus laxicarpicus* (a), (b), (g), (l) LE348807; (c)–(f), (h)–(j) HFNNU 12497; (m) MYX 23608). (a), (b) Mature sporocarps (DM). (c) Apical part of the sporocarp (LM). (d) Surface net (LM). (e), (f) Detail of the surface net (SEM). (g) Detail of the capillitium threads (SEM). (h) Capillitium in the middle part of the sporotheca (LM). (i) Capillitium in the middle part of the sporotheca (SEM). (j) Edge of the sporotheca (SEM). (k) Spores (LM). (l) Spore (SEM). (m) Detail of the spore ornamentation (SEM) Scale bars: (a), (b) = 3 mm; (c) = 200 μm; (d), (h), (i) = 100 μm; (j) = 50 μm; (e), (g), (k) = 10 μm; (f), (l) = 5 μm; (m) = 1 μm.

deciduous wood, 30 Jun 2022, field, leg. Bortnikova N.A. (LE348807, GenBank *nrSSU*: PX940077; *EF-1α*: PX961587; *mtSSU*: PX940090).

Diagnosis: Sporocarps densely to loosely gregarious, (6.1–)6.4–7.1(–8.1) mm in total height; stalk relatively long (25%–40% of the total height); surface net with filamentous to flattened-band-shaped threads, meshes (6–)10–17(–27) μm in diameter, the threads abundantly bearing spines; and spores (5.7–)6.6–7.2(–7.9) μm in diameter, ornamented with nearly uniformly distributed bacula of unequal size.

Description: Sporocarps erect, stalked, densely to loosely gregarious, (6.1–)6.4–7.1(–8.1) mm in total height. Sporotheca elongate-cylindrical, tapering towards both ends, apex bluntly rounded, strong brown to deep orange brown, 0.3–0.4 mm wide. Stalk black, shiny, 2.0–2.5(–2.7) mm long, 25%–40% of the total height, base forming a short cone. Hypothallus membranous, silvery white, shiny, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex, unbranched. Capillitium arising perpendicularly from the entire length of the columella, with a large triangular expansion at the point of origin, dense in the middle, sparser at the base and apex, nearly black to light orange, branching complex, with irregular membranous expansions at the branching points, threads nearly smooth or with irregular small warts, connecting to the surface net. Surface net well-developed, generally complete, sometimes slightly incomplete especially at the sporotheca apex; threads filamentous to flattened-band shaped, often with membranous expansions at the branching points; meshes dense, irregularly polygonal, (6–)10–17(–27) μm in diameter, threads ornamented with irregularly distributed small warts, sometimes clustered, and irregularly bearing spines of variable length projecting outwards from the sporotheca. Spore concolorous with the sporotheca in mass, brown or lighter in transmitted light, globose to subglobose, (5.7–)6.6–7.2(–7.9) μm in diameter, ornamented with nearly uniformly distributed bacula of unequal size; secondary ornamentation barely visible to rough and finely verrucous. Plasmodium not observed.

Additional materials examined: CHINA, Henan Province, Nanyang City, Baotianman National Nature Reserve, on rotten wood, 23 Jun 2025, field, leg. Gao Y. and Wang G.W. (HFNNU 12497). **RUSSIA**, Moscow, Orekhovo-Borisovo, between buildings 23-1 and 25 on Orekhovy Boulevard, 55.6132° N, 37.7264° E, on rotten, painted or otherwise treated wooden fragments from a playground, 21 Aug 2023, field, leg. Gmoshinskiy V.I. and Kireeva N.I. (MYX 23608).

Distribution: currently known from Central China and European and Far Eastern Russia.

Habitat: on rotten wood.

Notes: *Symphytocarpus laxicarpicus* is morphologically most similar to *Cor. pallida*. The two differ consistently in spore ornamentation and sporotheca color. The bacula on the spores of *Cor. pallida* bear distinct apical thickening (see Moreno et al.[71]: fig. 8h), whereas those of *Sym. laxicarpicus* lack such structures (Fig. 35l), with secondary ornamentation barely visible to rough, and are finely

verrucous (Fig. 35m). Furthermore, the sporotheca of *Cor. pallida* is typically blackish brown[83], while that of *Sym. laxicarpicus* is more vividly colored, ranging from strong brown to deep orange to moderate yellowish pink (Fig. 35a, b). The newly described *Sym. uniforatus* in this study is also morphologically similar but differs in its proportionally shorter stalk (only 15%–30% of the total height) and its surface net threads, which lack spines.

Phylogenetically, *Sym. laxicarpicus* forms an independent, well-supported clade (UBS/PP/TBE = 100/100/100; Fig. 1) and is not sister to any other known or newly described species in this study. It shows closer affinity to *Sym. tenuipes* and *Sym. minor*, but is distinguished morphologically: *Sym. tenuipes* has taller sporocarps ([9.4–]10.6–15.8[–16.6] mm), a columella with an apical membranous expansion or thickening, and larger spores ([6.9–]7.5–8.0[–8.5] μm in diameter); whereas *Sym. minor* has a notably sparser capillitium with less conspicuous membranous expansions at the branching points. Based on its unique combination of morphological characteristics and phylogenetic position, *Sym. laxicarpicus* is confirmed as a new species.

Symphytocarpus microsporus **(Nann.-Bremek. & Y. Yamam.) W.L. Song, Bortnikov, Gmoshinskiy, Shuang-Lin Chen & Novozh., comb. & stat. nov.** **Fig. 36**

MycoBank number: MB863336.

Basionym: *Stemonitis aequalis* var. *microspora* Nann.-Bremek. & Y. Yamam., Proc. Kon. Ned. Akad. Wetensch., C 86: 237 (1983).

Etymology: *microsporus* (Latin), from the Greek *mikros* (small) and *spora* (seed, spore), referring to the characteristically small spore of this species.

Materials examined: JAPAN, Kochi Prefecture, Moyoyama-cho, Sogauchi, on rotten wood, 20 Jul 1980, field, leg. Yamamoto Y. (holotype, TNS-M-Y-22052 = YY-626).

Notes: *Stemonitis aequalis* var. *microspora* was described from Japan[99] and is currently regarded as a synonym of *Stp. aequalis*[6]. Examination of the holotype (TNS-M-Y-22052 = YY-626; Fig. 36) revealed it to be in poor condition and heavily contaminated with fungi, preventing DNA extraction and sequencing. Nevertheless, a detailed morphological study provided new data that differ in part from the protologue[99]. New measurements of the holotype are: sporocarps (2.8–)2.9–3.5(–3.6) mm in total height and 0.3–0.4 mm in width; stalk (0.7–)1.0–1.2(–1.4) mm long (25%–43% of the total height); spores (5.0–)6.0–6.6(–7.1) μm in diameter. The sporocarps are notably shorter, and the spores distinctly larger, than reported in the protologue (sporocarps 4–5 mm tall, ca. 0.4 mm wide; stalk about 1/3 of the height; spores (4.0–)4.5–5.0(–6.0) μm).

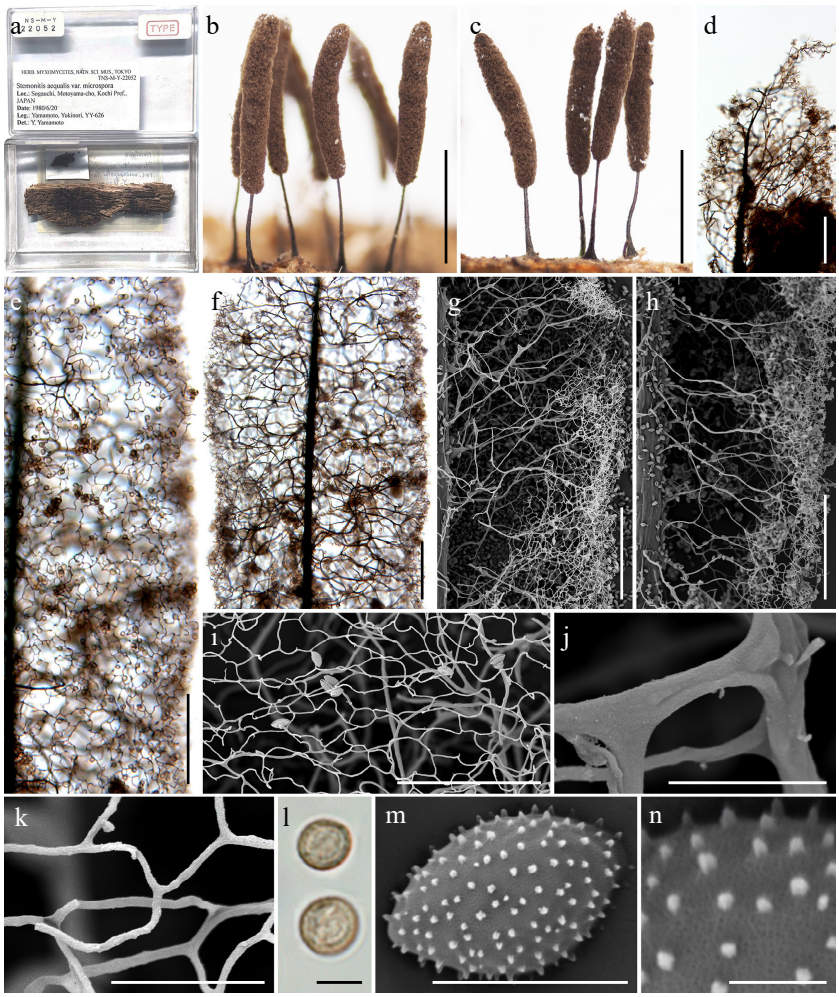

Fig. 36 Morphological characteristics of the holotype (TNS-M-Y 22052 = YY-626) of *Symphytocarpus microsporus* (≡ *Stemonitis aequalis* var. *microspora*). (a) Herbarium labels and interior views of the herbarium box containing the holotype. (b), (c) Mature sporocarps (DM). (d) Apical view of the sporotheca (LM). (e) Surface net (LM). (f) Capillitium in the middle part of the sporotheca (LM). (g), (h) Capillitium in the middle part of the sporotheca (SEM). (i) Detail of the surface net (SEM). (j) Detail of the capillitium threads (SEM). (k) Detail of the surface net (SEM). (l) Spores (LM). (m) Spore (SEM). (n) Detail of the spore ornamentation (SEM). Scale bars: (b), (c) = 2 mm; (d)–(h) = 100 μm; (i) = 50 μm; (j), (k) = 10 μm; (l)–(n) = 5 μm.

Morphologically, the surface net is incomplete and wavy, with meshes (6–)10–22(–38) μm in diameter, matching the protologue. The threads of both the capillitium and surface net are nearly smooth, lacking conspicuous warts (Fig. 36j, k). Branching points of the capillitium sometimes bear irregular, membranous expansions, which may appear fusiform when less developed (Fig. 36j). Crucially, SEM reveals that the spore surface consists not only of the typical bacula but also a delicate reticulum formed by dense, circular pores, visible only under SEM (Fig. 36l–n). This combination of reticulate spores and pale sporocarp coloration aligns with the emended concept of *Symphytocarpus*. Although the new measurements diverge from the protologue, the holotype differs substantially from *Stp. aequalis* in spore size and sporocarp proportions. Therefore, it is recognized as a distinct species and transferred to *Symphytocarpus* with elevation to species rank as *Sym. microsporus*.

***Symphytocarpus minor* Bortnikov, W.L. Song, Shuang L. Chen & Novozh., sp. nov. Fig. 37**

MycoBank number: MB863305.

Etymology: *minor* (Latin), meaning *smaller*; referring to the consistently smaller dimensions of this species compared to the closely related *Sym. splendens* in key diagnostic characteristics, including total sporocarp height, surface net mesh diameter, spore diameter, and spore ornamentation.

Holotype: RUSSIA, Jewish Autonomous Region, Obluchensky District, Bastak Nature Reserve, 49.1256° N, 133.1327° E, on decayed deciduous wood, 28 Jun 2022, field, leg. Bortnikova N.A. (LE348776, GenBank *nrSSU*: PZ165565; *EF-1α*: PZ188765; *mtSSU*: PZ160568).

Diagnosis: Sporocarps moderately gregarious, (4.5–)5.3–8.6(–9.5) mm in total height, slender, about 0.2–0.4 mm wide, stalk 30%–40% of the height; capillitium usually lax, poorly developed; surface net well-developed, with meshes (8–)13–30(–52) μm in diameter and rare free tips; spores (5.8–)6.4–7.2(–7.6) μm in diameter with poorly developed secondary ornamentation.

Description: Sporocarps erect, stalked, gregarious in small groups, (4.5–)5.3–8.6(–9.5) mm in total height. Sporotheca elongate-cylindrical, tapering upwards and sometimes downwards, apex bluntly rounded, dark orange-brown to brown, 0.2–0.3(–0.4) mm wide. Stalk black, shiny, about 30 μm wide, (1.1–)1.5–2.9(–3.5) mm long, (25%–)28%–39%(–43)% of the total height, base conical. Hypothallus membranous, translucent or silvery to yellowish brown and brown, common to the colony, usually thin and lighter between dark stalk bases, sometimes also with dark lines separating the areas around each sporangium. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex and slightly sinuous. Capillitium with main branches, brown, rarely branched, forming a very lax internal net with frequent membranous expansions at the branching points; connecting to the surface net; smooth by LM

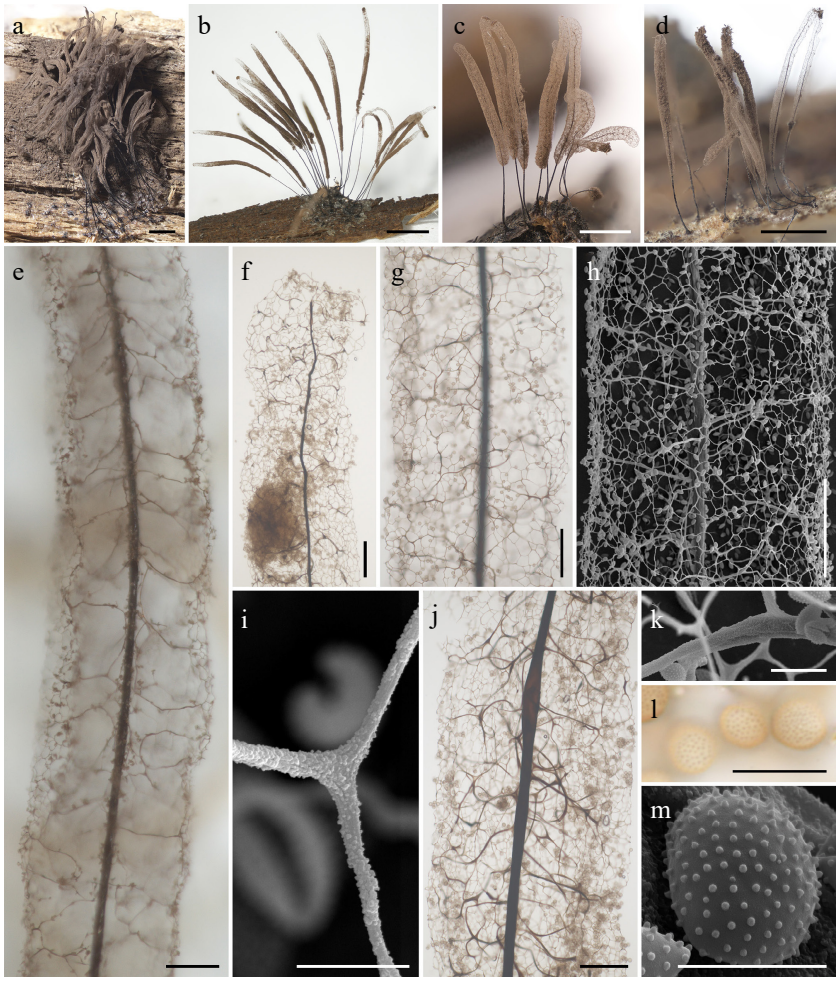

Fig. 37 Morphological characteristics of *Symphytocarpus minor* (a), (j) LE306599; (b), (l) LE348772; (c), (e), (g)–(i), (k), (m) LE348776; (d), (f) LE307469. (a)–(d) Mature sporocarps (DM). (e) Capillitium in the middle part of the sporotheca (LM). (f) Apical region of the sporocarp (LM). (g) Surface net (LM). (h) Surface net (SEM). (i) Detail of the surface net (SEM). (j) Capillitium in the middle part of the sporotheca (LM). (k) Detail of the capillitium threads (SEM). (l) Spores (LM). (m) Spores (SEM). Scale bars: (a)–(d) = 2 mm; (e), (f), (g), (h) = 100 μm; (j) = 50 μm; (k), (l) = 10 μm; (i), (m) = 5 μm.

but minutely verrucose under SEM. Surface net well-developed, evanescent at the sporotheca apex but complete elsewhere; meshes irregularly polygonal to circular, (8–)13–30(–52) μm in diameter with rare spiny tips of variable length. Spore concolorous with the sporotheca in mass, pale brown in transmitted light; spores globose to subglobose, (5.8–)6.4–7.2(–7.6) μm in diameter, distinctly ornamented with uniformly distributed bacula; secondary surface ornamentation ranges from rough to very finely verrucous. Plasmodium not observed.

Additional materials examined: RUSSIA, Murmansk Region, Monchegorsk Municipal District, Laplandskiy State Nature Biosphere Reserve, 67.6705° N, 32.4289° E, on decayed wood of *Picea obovata*, 26 Aug 2015, field, leg. Novozhilov Yu.K., Shchepin O.N., Erastova D.A., and Tikhonova E.N. (LE306599); Leningrad Region, Lodeynopolsky District, Nizhne-Svirsky Nature Reserve, 60.6667° N, 33.2500° E, on decayed wood of *Picea abies*, 8 Jul 2015, field, leg. Novozhilov Yu.K., Shchepin O.N. and Erastova D.A. (LE307469); Jewish Autonomous Region, Obluchensky District, Bastak Nature Reserve, 49.1256° N, 133.1327° E, on decayed deciduous wood, 28 Jun 2022, field, leg. Bortnikova N.A. (LE348772).

Distribution: currently known from European and Far Eastern Russia.

Habitat: on rotten wood.

Notes: *Symphytocarpus minor* shares with *Sym. splendens* a well-developed surface capillitial net combined with a lax internal net. Nevertheless, *Sym. minor* differs from *Sym. splendens* in the following key characteristics: 1) total sporocarp height: 4.5–9.5 mm vs 15–25 mm; 2) surface net meshes are mostly < 30 μm vs mostly > 30 μm; 3) spore diameter 5.8–7.6 μm vs 7.2–9.1 μm; 4) spore secondary ornamentation: barely visible vs distinct fine reticulum.

Phylogenetic analyses indicate that *Sym. minor* forms a well-supported sister clade (UBS/PP/TBE = 100/100/100; Fig. 1) with *Sym. tenuipes*. Despite this close phylogenetic relationship, *Sym. minor* differs from *Sym. tenuipes* by multiple morphological traits: 1) total height of sporocarps (4.5–)5.3–8.6(–9.5) mm vs (9.4–)10.6–15.8(–16.6) mm; 2) stalk length (1.1–)1.5–2.9(–3.5) mm vs (2.7–)3.9–5.5(–5.8) mm; 3) columella without membranous expansion vs columella with a distinct membranous expansion (or slightly thickened if expansion inconspicuous); 4) capillitium density and branching: main branches rarely branched; internal net very lax, poorly developed vs dense, much and intricately branched near columella and sporotheca margin; 5) spore diameter (5.8–)6.4–7.2(–7.6) μm vs (6.9–)7.5–8.0(–8.5) μm.

Symphytocarpus planus (B. Zhang & Yu Li) Bortnikov, W.L. Song & Novozh., comb. nov.

MycoBank number: MB863337.

Basionym: *Stemonitis plana* B. Zhang & Yu Li, Phytotaxa 323 (1): 84 (2017).

Notes: *Stemonitis plana* was described based on a specimen collected from China[130]. It was originally published as *Stemonitis planusis* but was later corrected to *Ste. plana* in MycoBank and the online nomenclatural information system of Eumycetozoa[6]. The transfer of this species to *Symphytocarpus* is justified by the following morphological characteristics: densely gregarious sporocarps with a brown to dark-brown sporotheca; spore ornamentation consists of bacula, overlaid by a dense, delicate reticulum (see Zhang & Li[130]: fig. 2d). This combination of characteristics matches the emended concept of *Symphytocarpus*, justifying the new combination *Sym. planus*. The protologue was based on a single specimen, and the flattened sporotheca apex, from which the epithet is derived, was treated as diagnostic. However, observations across related taxa suggest this characteristic may be variable and requires further study.

This species may also show some similarity to *Sym. rhizoideipes* (≡ *Ste. rhizoideipes*) from India[24]. Both have a sparse capillitium and an irregular surface net with comparable mesh dimensions, and their spore diameters are similar. However, *Sym. plana* has much smaller sporocarps (10–13 mm in total height vs 16–20 mm in *Sym. rhizoideipes*), and its protologue makes no mention of the oblong or oval peridial fragments (20–30 μm wide, 20–100 μm long) described for *Sym. rhizoideipes*[24] and also reported by Vlasenko et al.[131]. Interestingly, the spore ornamentation of *Sym. plana* (see Zhang & Li[130]: fig. 2d) closely resembles that illustrated for *Sym. rhizoideipes* by Vlasenko et al.[131]. Examination of the respective type specimens is needed to clarify the relationship between these two taxa.

Symphytocarpus pseudoflavogenitus (A. Vlasenko & Novozh.) W.L. Song, Bortnikov, Gmoshinskiy, A. Vlasenko, Novozh. & Shuang L. Chen, comb. nov. Fig. 38

MycoBank number: MB863338.

Basionym: *Stemonitis pseudoflavogenita* A. Vlasenko & Novozh., Phytotaxa 447(2):139 (2020).

Materials examined: CHINA, Gansu Province, Zhouqu County, 33.4900° N, 104.2100° E, on rotten wood, 17 Jul 1998, field, leg. Chen S.L. (HMAS 75457, HMAS 75422); Heilongjiang Province, Greater Khingan Range Prefecture, on rotten wood, 27 Jul 2024, field, leg. Chen S.L. and Yan S.Z. (HFNNU 11574, HFNNU 11433). **RUSSIA**, Volgograd Region, Sredneakhtubinsky District, vicinity of Kuropatka lake, 48.5864° N, 44.6586° E, on decayed log of *Quercus robur*, 26 Aug 2018, field, leg. Zemlyanskaya I.V. (LE279129); Krasnodar Territory, Kanevskoy District, 0.5 km northwest of the Kanevskaya village, 46.1072° N, 38.9317° E, on decayed deciduous wood, 5 Jun 2017, field, leg. Botyakov V.N. (isotype, LE319201); Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.9238° N, 158.7063° E, on decayed log of *Salix* sp., 14 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325162); Kamchatka Territory, Bystrinsky District, vicinity of Esso village, 55.9238° N, 158.7063° E, on decayed log of *Populus maximowiczii*, 14 Aug 2019, field, leg. Novozhilov Yu.K., Shchepin O.N., and Schnittler M. (LE325206); Yaroslavl Region, Pereslavl-Zalessky, Plesheevo Ozero National Park, 56.7264° N, 38.7594° E, on rotten wood, 24 Sep 2024, field, leg. Sakulin S.V. and Gmoshinskiy V.I. (MYX 24986); Tver Region, Nelidovsky Urban Okrug, Central Forest State Nature Reserve, 56.4710° N, 32.9925° E, on rotten wood, 05 Aug 2021, field, leg. Gmoshinskiy V.I. (MYX 22382); Republic of Mordovia, Ichalkovsky District, Smolnenskoye rural settlement, 54.8393° N, 45.2345° E, on rotten wood, 10 Jul 2021, field, leg. Sheremetyeva A.I. and Gmoshinskiy V.I. (MYX 19750).

Notes: *Stemonitis pseudoflavogenita* is a recently described species[69], characterized by an apical expansion of the columella and a complex spore ornamentation consisting of large warts with irregularly scattered warts and indentations. The morphological characteristics of the specimens studied here generally conform to the protologue[69]. However, it should be noted that at least one of the studied specimens, LE279129, has sporocarps of 8.6–9.7 mm in total height (vs 3–5 mm in the protologue), which may indicate either a certain degree of aberration of the original material, or a large morphological plasticity of this species. Additionally, in the Chinese specimens, the expansion of the columella at the sporotheca apex is variable in size and sometimes absent (Fig. 38d–i, n), with notable differences even among sporocarps from the same collection (Fig. 38e, h). It is also noted that the threads of both the capillitium and the surface net are densely ornamented with small warts (Fig. 38p, q), a stable characteristic observed in all examined

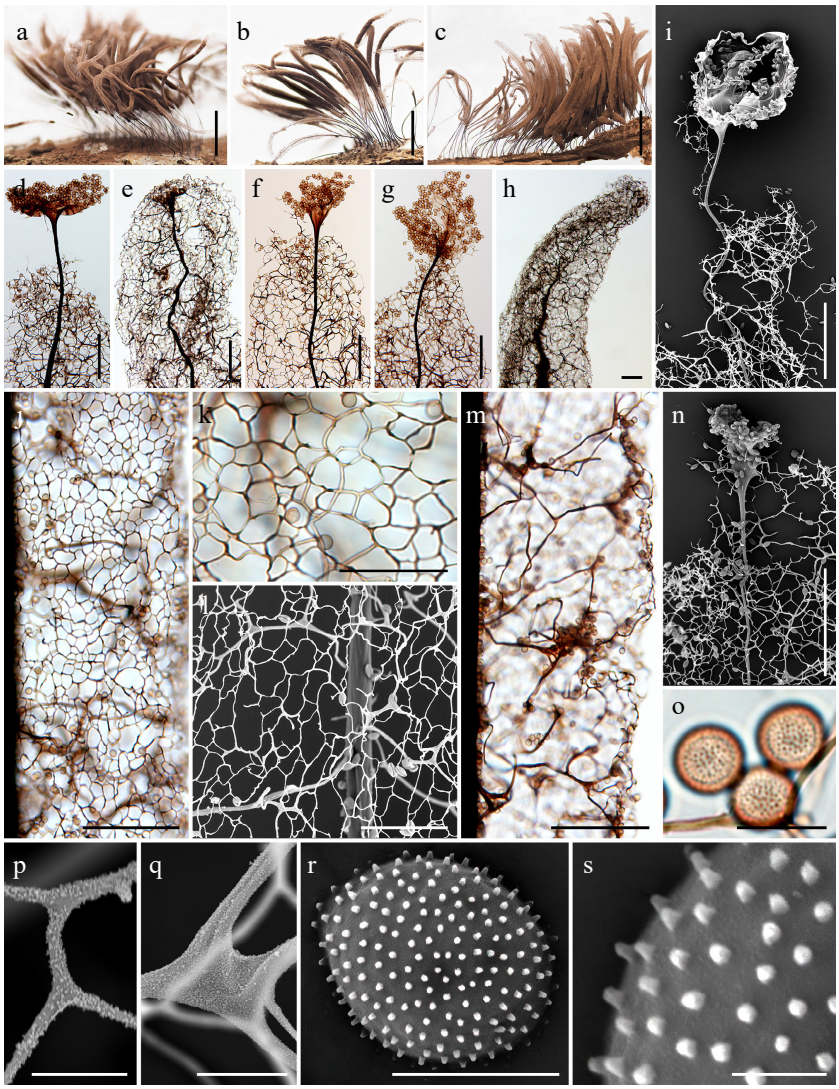

Fig. 38 Morphological characteristics of *Symphytocarpus pseudoflavogenitus* (a), (d), (f), (g), (i), (o)–(s) HFNNU 11433; (b), (l), (n) HFNNU 11574; (c), (e), (h), (j), (k), (m) HMAS 75422. (a)–(c) Mature sporocarps (DM). (d)–(h) Apical view of the sporotheca (LM). (i) Apical view of the sporotheca (SEM). (j) Surface net (LM). (k) Detail of the surface net (LM). (l) Detail of the surface net (SEM). (m) Capillitium in the middle part of the sporotheca (LM). (n) Apical view of the columella (SEM). (o) Spores (LM). (p) Detail of the surface net (SEM). (q) Detail of the capillitium threads (SEM). (r) Spore (SEM). (s) Detail of the spore ornamentation (SEM). Scale bars: (a)–(c) = 2 mm; (d)–(j), (m), (n) = 100 μm; (k), (l) = 50 μm; (q) = 10 μm; (p), (r) = 5 μm; (s) = 1 μm.

material. Thus, a more thorough study of this species in order to clarify the boundaries of the variability of morphological characteristics will be useful in the future.

The *nrSSU* sequences of the examined specimens are identical to that of the isotype (LE319201). In the three-gene phylogenetic tree, the studied specimens and the isotype form a well-supported clade (UBS/PP/TBE = 99/96/100, Fig. 1). This clade is closely related to the type of *Symphytocarpus*, *Sym. flaccidus,* forming a well-supported sister-group relationship (UBS/PP/TBE = 100/-/-). Given the morphological similarities (densely gregarious sporocarps, brown sporotheca, and spores with distinct or inconspicuous secondary ornamentation) and the phylogenetic evidence, *Ste. pseudoflavogenita* is transferred to *Symphytocarpus* as *Sym. pseudoflavogenitus*.

***Symphytocarpus rhizoideipes* (Nann.-Bremek., R. Sharma & K.S. Thind) W.L. Song, Bortnikov, Gmoshinskiy & A. Vlasenko, comb. nov.**

MycoBank number: MB863339.

Basionym: *Stemonitis rhizoideipes* Nann.-Bremek., R. Sharma & K.S. Thind, Proc. Kon. Ned. Akad. Wetensch., C. 87(4):465 (1984).

Notes: *Stemonitis rhizoideipes* was described from India[24]. The species is characterized by large sporocarps (16–20 mm in total height, 0.5–0.7 mm in diameter), a surface net with large meshes, a capillitium that is absent or nearly so, and the presence of large, oblong to oval peridial fragments (20–30 μm wide, 20–100 μm long). The species was later reported from Russia by Vlasenko et al.[131], whose illustrations and description match the protologue closely and confirm the identity. The SEM images provided by Vlasenko et al.[131] show that the spore ornamentation consists of irregularly distributed bacula overlaid by a dense, delicate reticulum. This combination of characteristics aligns with the morphological concept of *Symphytocarpus*. Therefore, *Ste. rhizoideipes* is transferred to *Symphytocarpus* as *Sym. rhizoideipes*.

Symphytocarpus rhizoideipes is morphologically similar to *Sym. planus* (≡ *Ste. plana*); for a distinction between the two, see the Notes for *Sym. planus*.

***Symphytocarpus rubescens* (Y. Yamam.) W.L. Song, Bortnikov, Gmoshinskiy, Novozh., & Shuang L. Chen, comb. & stat. nov. Fig. 39**

MycoBank number: MB863340.

Basionym: *Stemonitis pallida* var. *rubescens* Y. Yamam., Stapfia 73: 98 (2000).

Etymology: *rubescens* (Latin) becoming red, reddish, referring to the reddish-brown color of the sporotheca.

Materials examined: JAPAN, Kochi Prefecture, Kochi-shi, Otsu, on ligno carioso of *Pinus densiflora*, 31 Aug 1986, field, leg. Yamamoto Y. (holotype, TNS-M-Y-22055 = YY-4623).

Notes: *Stemonitis pallida* var. *rubescens* was described from Japan as a variety of *Ste. pallida* (≡ *Cor. pallida*)[112]. It was originally considered an intermediate form between *Sym. ferrugineus* (= *Ste. axifera*) and *Cor. pallida* (≡ *Ste. pallida*). New measurements of the holotype (TNS-M-Y-22055 = YY-4623; Fig. 39) are as follows: sporocarps (4.1–)4.7–6.1(–6.6) mm in total height, 0.3–0.5 mm in diameter; stalk (1.2–)1.6–2.3(–2.6) mm long (25%–50% of the total height); surface net meshes (8–)11–17(–24) μm in diameter; and spores (6.1–)6.8–7.4(–7.9) μm in diameter. These values are largely consistent with the original description[112], which reported sporocarps up to 9 mm in total height; stalk up to 3.5 mm long, about 1/3–1/2 of the total height; surface net meshes 8–20(–40) μm in diameter; and spores 6.1–7.7 μm in diameter.

Detailed examination of its holotype reveals a highly distinctive spore ornamentation: under SEM, the spores bear unevenly distributed bacula that are often clustered and are connected by short ridges, forming discontinuous crests; the entire surface is additionally overlaid by a dense, delicate reticulum (Fig. 39q, r). This is a relatively rare characteristic in *Symphytocarpus*. In contrast, *Cor. pallida* exhibits bacula with apically thickened tips (see Moreno et al.[71]: fig. 8h) and lacks a reticulum on the spore surface, indicating a significant morphological difference between the two taxa. Therefore, *Ste. pallida* var. *rubescens* should not be treated as a synonym of *Cor. pallida*.

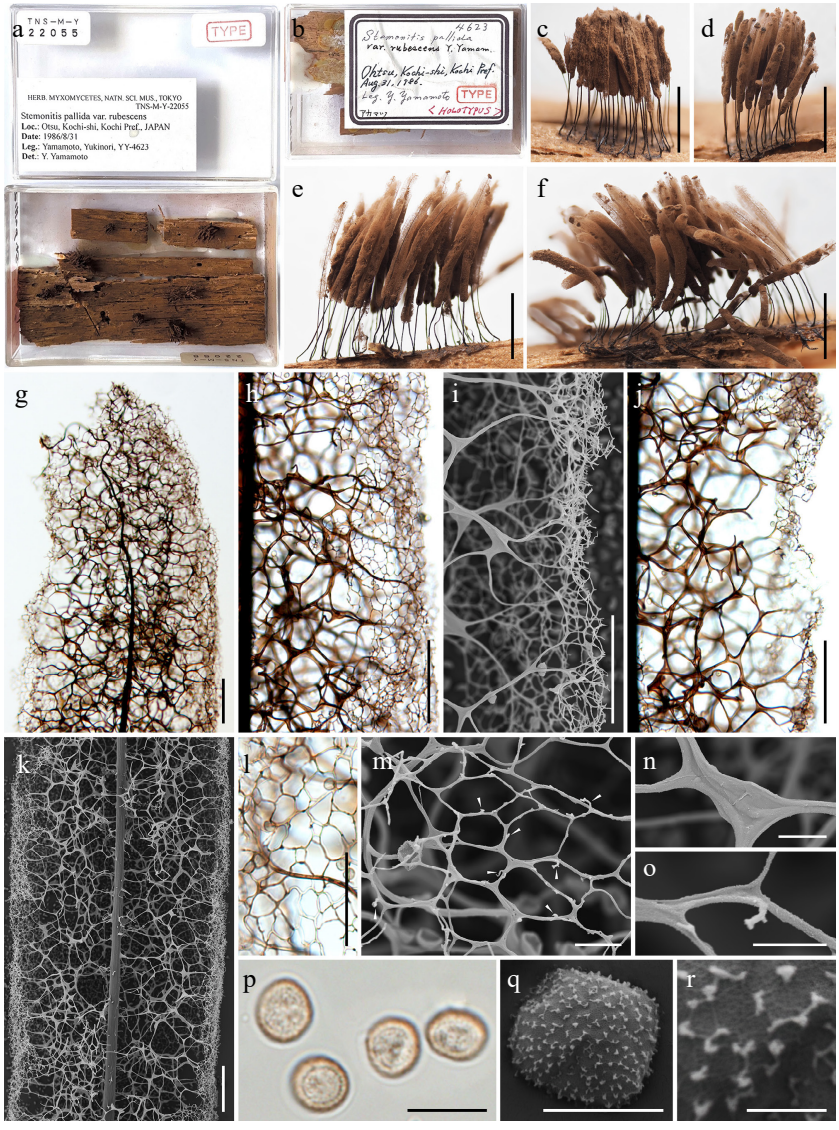

Fig. 39 Morphological characteristics of the holotype (TNS-M-Y-22055 = YY-4623) of *Symphytocarpus rubescens* (≡ *Stemonitis pallida* var. *rubescens*). (a) Herbarium labels and interior views of the herbarium box containing the holotypes. (b) Herbarium labels of the herbarium box containing the holotypes. (c)–(f) Mature sporocarps (DM). (g) Apical view of the sporotheca (LM). (h) Capillitium and surface net in the middle part of the sporotheca (LM). (i) Capillitium and surface net in the edge of the sporotheca (SEM). (j) Capillitium in the middle part of the sporotheca (LM). (k) Capillitium in the middle part of the sporotheca (SEM). (l) Surface net (LM). (m) Spines on the surface net (SEM, arrow). (n) Detail of the capillitium threads (SEM). (o) Detail of the surface net (SEM). (p) Spore (LM). (q) Spores (SEM). (r) Detail on the spore ornamentation (SEM). Scale bars: (c)–(f) = 3 mm; (g), (h), (j), (k) = 100 μm; (i), (l) = 50 μm; (m), (n), (p) = 10 μm; (o), (q) = 5 μm; (r) = 1 μm.

While *Sym. ferrugineus* shares the presence of unevenly distributed bacula and a dense, delicate reticulum, its bacula are not interconnected into ridges (Figs 32m, n; 33k; 34l), and its capillitium is notably sparser (Figs 32d, e; 33e–g; 34e) than that of *Ste. pallida* var. *rubescens*.

Based on these morphological distinctions, it is proposed that *Ste. pallida* var. *rubescens* represents a distinct species. Given that its spore ornamentation aligns well with the generic concept of *Symphytocarpus*, and considering its clustered sporocarps with pale coloration, *Ste. pallida* var. *rubescens* is formally transferred to *Symphytocarpus* and elevated to species rank as *Sym. rubescens*.

***Symphytocarpus sichuanensis* (B. Zhang & Yu Li) Bortnikov, W.L. Song & Novozh., comb. nov.**

MycoBank number: MB863341.

Basionym: *Stemonitis sichuanensis* B. Zhang & Yu Li, Phytotaxa 258 (2): 196 (2016).

Notes: *Stemonitis sichuanensis* was described based on specimens from China[113]. Its spore ornamentation consists of typical bacula overlaid by a dense, delicate reticulum (see Zhang & Li[113]: fig. 1f). The columella often bears an expansion (see Zhang & Li[113]: fig. 1c, e), a potentially diagnostic characteristic. However, as similar columella polymorphism occurs in *Sym. splendens* (see below) and *Sym. pseudoflavogenitus*, re-examination of the type or fresh material of *Ste. sichuanensis* is recommended. Nevertheless, the spore morphology aligns closely with the emended concept of *Symphytocarpus*. Therefore, *Ste. sichuanensis* is transferred to *Symphytocarpus* as *Sym. sichuanensis*.

***Symphytocarpus splendens* (Rostaf.) W.L. Song, Bortnikov, Gmoshinskiy, Shuang L. Chen & Novozh., comb. nov. Figs 40–42**

MycoBank number: MB863342, **MycoBank typification number:** MBT10032401.

Basionym: *Stemonitis splendens* Rostaf., Pamiętn. Towarz. Nauk Ścisłych Paryżu 5 (4): 195 (1874).

Materials examined: RUSSIAN EMPIRE, (surroundings of St. Petersburg or Little Russia, around 1820–1835, the substrate is unknown), Herb. Acad. Sc. Petropol., Herb. Bongard, as '*Stemonitis gracilis* Bong. in herb.'; det. as *Comatricha longa* Peck (and later redet. as *Stemonitis splendens* Rost.) by A.A. Jaczewski, det. as '*S. splendens* Rost.?' by W.H. Tranzschel; with a note 'Rostafinski vidit 1873'; №1246 (early herbarium numbering by Novozhilov Yu.K.) (lectotype, designated by Bortnikov F.M., Gmoshinskiy V.I. and Song W.L. here, LE46378). **BELARUS**, Gomel Region, Zhytkavichy District, Pripyatsky National Park, vicinity of Hlupin village, 52.0492° N, 28.0929° E, on rotten wood, 16 Aug 2022, field, leg. Moroz E.L. (MSK-F 43601). **CHINA**, Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, on rotten wood, 20 Jul 2024, field, leg. Song W.L., Meng Q., and Chen Y.J. (HFNNU 10977); Jiangsu Province, Nanjing City, Zijin Mountain National Forest Park, on rotten wood, 21 Jul 2024, field, leg. Song W.L., Meng Q., and Chen Y.J. (HFNNU 10990); Heilongjiang Province, Greater Khingan Range Prefecture, Jiagedaqi National Forest Park, on rotten wood, 31 Jul 2024, field, leg. Chen S.L., and Yan S.Z. (HFNNU 11576); Hubei Province, Yichang City, Houhe National Nature Reserve, on rotten wood, 20 Jul 2019, field, leg. Li M. (HFNNU 12500); Henan Province, Nanyang City, Baotianman National Nature Reserve, on rotten wood, 23 Jun 2016, field, leg. Gao Y. and Wang G.W. (HFNNU 13261); Henan Province, Nanyang City, Baotianman National Nature Reserve, on rotten wood, 27 Aug 2016, field, leg. Gao Y. and Wang G.W. (HFNNU 13262); Jiangxi Province, Pingxiang City, Bihutan National Forest Park, on rotten wood, 15 Jul 2022, field, leg. Chen S.L., Yan S.Z. (HFNNU 4191);

Fig. 40 Herbarium envelope and mature sporocarps of the lectotype (LE46378) of *Symphytocarpus splendens*. (a) Herbarium labels and interior views of the herbarium box containing the lectotype. (b) The interior views of the herbarium box. (c) The notes 'Herb. Bongard' and 'Rostafinski vidit 1873'. (d), (e) Mature sporocarps (DM). (f) Apical view of the sporotheca (DM). (g) Hypothallus (DM). Scale bars: (d), (e) = 2 mm; (f), (g) = 1 mm.

Henan Province, Nanyang City, Baotianman National Nature Reserve, 33.0502° N, 111.8385° E, on rotten wood, 28 Jul 2015, field, leg. Gao Y. and He G. (HMAS 0258263); Henan Province, Luoyang City, Longyuwan National Forest Park, 34.6652° N, 112.3826° E, on rotten wood, 31 Jul 2015, field, leg. Gao Y. and He G. (HMAS 0258301, HMAS 0258304); Henan Province, Xinyang City, Dongzhai National Nature Reserve, 31.4541° N, 114.2015° E, on rotten wood, 17 Aug 2020, field, leg. Du Q. (HMAS 0294767, HMAS 0294776); Hubei Province, Macheng City, Wunao Mountain National Forest Park, 31.2281° N, 114.9875° E, on rotten wood, 15 Jul 2021, field, leg. Du Q. (HMAS 0295148, HMAS 0295149); Hubei Province, Macheng City, Fuchiao River National Wetland Park, 31.1816° N, 114.8757° E, on rotten wood, 15 Jul 2021, field, leg. Du Q. (HMAS 0295150); Hubei Province, Macheng City, Fuchiao River National Wetland Park, 31.1818° N, 114.8745° E, on rotten wood, 15 Jul 2021, field, leg. Du Q. (HMAS 0295162); Anhui Province, Anqing City, Tianzhu Mountain National Forest Park, 30.7036° N, 116.4653° E, on rotten wood, 18 Oct 2021, field, leg. Du Q. (HMAS 0295468); Hunan Province, Zhangjiajie City, on rotten wood, 9 Aug 1997, field, leg. Wang D.P. (HMAS 72195); Hunan Province, Zhangjiajie City, on a dead twig, 11 Aug 1997, field, leg. Wang D.P. (HMAS 72488, HMAS 72518); Hong Kong Special Administrative Region, on dead bark, 20 Jul 1998, field, leg. Zhuang W.Y. (HMAS 74774); Beijing City, Mentougou District, Dongling Mountain National Forest Park, 39.5500° N, 116.2400° E, on dead bark, 18 Aug 1998, field, leg. Chen S.L. (HMAS 78091). **RUSSIA**, Volgograd Region, Sredneakhtubinsky District, vicinity of Kuropatka lake, 48.5883° N, 44.6589° E, on decayed stump of *Salix alba*, 18 Jun 2006, field, leg. Zemlyanskaya I.V. (LE274793); Primorye Territory, Khasansky District, Kedrovaya Pad Nature Reserve, 43.1142° N, 131.4560° E, on decayed deciduous wood, 15 Jul 2020, field, leg. Bortnikova N.A. (LE327953); Republic Mordovia, Ichalkovsky, Smolnenskoye rural settlement, 54.7263° N, 45.2345° E, on rotten wood, 26 Jun 2021, field, leg. Sheremetyeva A.I. and Gmoshinskiy V.I. (MYX 19746); Republic Mordovia, Ichalkovsky, Kemlyanskoye rural settlement, 54.7263° N, 45.2344° E, on rotten wood, 10 Jul 2021, field, leg. Sheremetyeva A.I. and Gmoshinskiy V.I. (MYX 19796); Moscow, Orekhovo-Borisovo, between houses 30 and 32 on Borisovsky Proezd, 55.6205° N, 37.7274° E, on dead fragments of the bark of a living, free-standing tree, 30 Jun 2024, field, leg. Gmoshinskiy V.I. and Kireeva N. (MYX 25029).

Lectotype condition: The specimen consists of three tufts, including more than 60 sporocarps, which, although depressed due to storage in an envelope and devoid of the main mass of spores, are nevertheless in good condition. The grey color of some areas of the capillitium and some spores appears to be due to fading over time or storage conditions.

Description of lectotype LE46378: Sporocarps in dense colonies, cylindrical, about 18–23 mm in height, 0.35–0.45 mm in width, more or less erect, or slightly curved (Fig. 40b–e). Hypothallus well developed, common to the colony, orange-brown to dark brown, shiny (Fig. 40g). Stalk hollow, about 2.5–4.0 mm in length (13%–20% of the total length of the sporangium), reddish-brown to dark brown or almost black, smooth and shiny, about 43–57 μm thick, usually expanded as a cone at the base sometimes to 180–230 μm. Columella concolorous with stalk, shiny, reaches almost the top of sporotheca and gradually tapers upward up to 10–5 μm, in the upper part (2–2.5 mm) sinuous (Figs 40f, 41e). Capillitium brown, sometimes faded to grayish-black, arising along the entire length of the columella, the main branches extend sideways or slightly downward, which is more pronounced in the upper part of the sporotheca; the internal net poorly developed, usually consists of main branches that branch only one or two times, turning into a surface network, and sometimes have membranous extensions at the base or at the branching points (Fig. 41f–h). Surface net well-developed, complete, with large meshes, (21–)37–69(–109) μm (n = 270); at the top and at the base of the sporotheca, the surface net often destroyed (Fig. 41a–d). Spores in mass apparently brown, some faded to gray; yellowish-brown, brownish to grayish in transmitted light, globose or subglobose (wall is somewhat unevenly thickened), (7.2–)7.9–8.6(–9.1) μm in diameter (mean = 8.23, SD = 0.35, n = 187), rather evenly ornamented with small but distinct warts (LM; Fig. 41i, j); ornamented by regularly distributed short bacula, and with a dense, delicate reticulum on the spore surface (SEM; Fig. 41k).

Notes: *Stemonitis splendens* was first described by Rostafinsky[132] in his monograph (see Rostafinsky[132]: p. 195, p. 418, Tab. XIII fig. 2). In the protologue, Rostafinsky listed three syntypes: a Funck exsiccates (Germany, Funck, Crypt. Gew. Bes. Fichtelgeb. Ed. II, No. 590, as *Ste. fasciculata*), a specimen from August Gustav Heinrich von Bongard's herbarium, and a collection from François Mathias René Leprieur from French Guiana.

In Bongard's herbarium (now in LE), three specimens of *Stemonitis* spp. were found: *Stemonitis ovata* var. *atrofusca* (Pers.) Pers. (= *Comatricha nigra* [Pers. ex J.F. Gmel.] J. Schröt.), *Stemonitis fasciculata* Pers. ex J.F. Gmel. (identified by Rostafinsky as *Ste. fusca* Roth; the present study confirms that the spores are definitely warted-reticulate), and '*Stemonitis gracilis* Bong. in herb'., described above, which is undoubtedly a syntype of *Ste. splendens* mentioned by Rostafinski; is also mentioned by Jaczewski's monograph, which was probably mistakenly initially identified by him as *Comatricha longa* Peck[133], but later the definition was corrected to *Ste. splendens* (Fig. 40a). Because the H.C. Funck exsiccate is rare and the Guiana material (if preserved) potentially may represent a different taxon, specimen LE46378 (the Bongard specimen) is designated as the lectotype of *Ste. splendens*, enabling a stable morphological concept and further epitypification with fresh European material for phylogenetic study.

The lectotype and modern specimens from Belarus to China share the following diagnostic combination: large gregarious sporocarps (Fig. 42a–d); a well-developed surface net with large meshes and no free tips, the threads bearing dense, unevenly distributed small warts but no spines (Fig. 42l–t); a capillitium that varies from sparse to relatively dense, its threads often minutely warted (visible under SEM; Fig. 42i–m); and spores about 8–8.5 μm in diameter, ornamented with uniformly distributed small bacula overlaid by a fine, pore-like reticulum (visible under SEM; Fig. 42u–x). Considerable variation occurs in sporocarps' total size, columella termination at the sporotheca apex (e.g., sinuous, gradually dissipating, or with a slight lamellate expansion; Fig. 42e–h), capillitium density, and the presence/absence of membranous expansions at branching points.

The consistent spore ornamentation supports the synonymy of *Ste. webberi* Rex with *Ste. splendens* (as treated by most recent authors), whereas *Ste. morganii* Peck, reported to lack the distinct, fine reticulum, may warrant separate status. Study of fresh North American material (including var. *morganii* (Peck) Torrend and var. *webberi* (Rex) Lister) is needed to clarify these relationships.

In the three-gene phylogeny (Fig. 1), all specimens identified as *Ste. splendens* forms a well-supported monophyletic clade (UBS/PP/TBE = 88/-/94), sister to *Sym.* aff. *flaccidus* (UBS/PP/TBE = 100/100/100). The shared morphological characteristics (gregarious habit, pale sporotheca, spores with a distinct secondary ornamentation) align with the emended concept of *Symphytocarpus*. Therefore, *Ste. splendens* is transferred to *Symphytocarpus* as *Sym. splendens*.

Symphytocarpus tenuipes **Bortnikov, W.L. Song, Novozh. & Shuang L. Chen, sp. nov. Fig. 43**

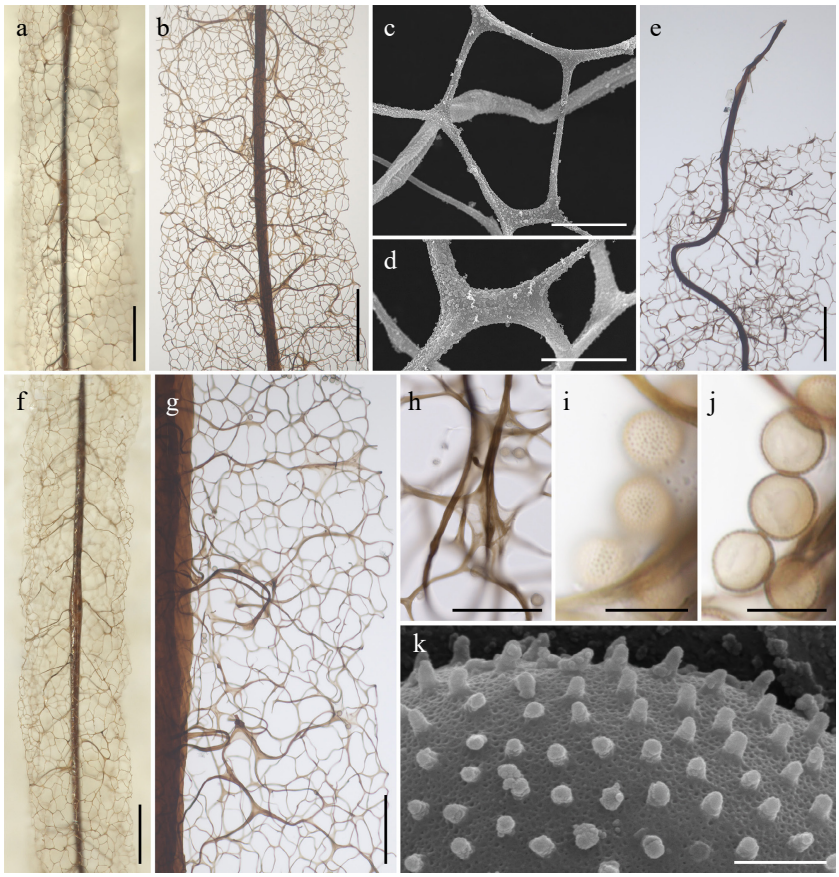

Fig. 41 Morphological characteristics of the lectotype (LE46378) of *Symphytocarpus splendens*. (a) Surface net (DM). (b) Surface net (LM). (c), (d) Detail of the surface net (SEM). (e) Apical view of the sporotheca (LM). (f) Capillitium and surface net in the middle part of the sporotheca (DM). (g) Capillitium and surface net in the middle part of the sporotheca (LM). (h) Extensions of the internal capillitium (LM). (i), (j) Spores (LM). (k) Detail of the spore ornamentation (SEM). Scale bars: (a), (b), (f) = 200 μm; (e), (g) = 100 μm; (c), (d), (h)–(j) = 10 μm; (k) = 1 μm.

MycoBank number: MB863125.

Etymology: *tenuipes* (Latin), from *tenuis* (thin, slender) and pes (foot, stalk), meaning 'with a slender stalk'; referring to the characteristically thin and delicate stalk of the sporocarps in this species.

Holotype: **RUSSIA**, Karachayevo-Circassian Republic, Karachayevsky District, Teberda Nature Reserve, 43.4410° N, 41.7248° E, on decayed wood of *Abies nordmaniana*, 7 Jun 2012, field, leg. Novozhilov Yu.K., Schnittler M. and Erastova D.A. (LE289716, GenBank *nrSSU*: PZ165614; *EF-1α*: PZ188805; *mtSSU*: PZ160621).

Diagnosis: Sporocarps (9.4–)10.6–15.8(–16.6) mm in total height; columella that reaches the apex of the sporotheca, often with a membranous expansion, or only slightly thickened when the expansion is not pronounced; surface net threads densely covered with irregular small warts and lacking spines; and spores (6.5–)7.5–8.0(–8.9) μm in diameter, ornamented with nearly uniformly distributed bacula, and sparse, flattened warts.

Description: Sporocarps erect, stalked, densely gregarious, (9.4–)10.6–15.8(–16.6) mm in total height. Sporotheca elongate-cylindrical, apex bluntly rounded, strong brown to deep brown, 0.2–0.4 mm wide. Stalk black, shiny, (2.7–)3.9–5.5(–5.8) mm long, 25%–50% of the total height, base forming a short cone; stalk sometimes very thin, (13–)21–43(–46) μm, to almost hairy and drooped under the weight of the sporotheca. Hypothallus membranous, silvery white to translucent, shiny, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex, with a membranous expansion or slightly thickened if the expansion is inconspicuous. Capillitium arising perpendicularly from the entire length of the columella, dense, strong brown to moderate orange, with a triangular expansion at the point of origin, much and intricately branched near the columella and sporotheca margin, scarcely branched elsewhere, with irregular membranous expansions at the branching points, threads densely covered with small warts or nearly smooth, connecting to the surface net. Surface net well-developed, often slightly incomplete at the sporotheca apex but complete elsewhere, threads filamentous, sometimes with membranous expansions at the branching points, meshes irregularly polygonal to circular, (14–)23–35(–63) μm in diameter, threads densely covered with irregular small warts, without spines. Spore concolorous with the sporotheca in mass, brown or lighter in transmitted light, globose to subglobose, (6.9–)7.5–8.0(–8.5) μm in diameter, ornamented with nearly uniformly distributed bacula, the spore surface bearing sparse, flattened, small warts, not forming a dense reticulum. Plasmodium not observed.

Additional materials examined: **RUSSIA**, Karachayevo-Circassian Republic, Karachayevsky District, Teberda Nature Reserve, 43.4381° N, 41.7178° E, on decayed wood of *Abies nordmaniana*, 30 May 2011, field, leg. Novozhilov Yu.K., Schnittler M. (LE285125); Karachayevo-Circassian Republic, Karachayevsky District, Teberda Nature Reserve, 43.4410° N, 41.7248° E, on decayed wood of *Abies nordmaniana*, 7 Jun 2012, field, leg. Novozhilov Yu.K., Schnittler M. and Erastova D.A. (LE289704); Karachayevo-Circassian Republic, Karachayevsky District, Teberda Nature Reserve, 43.4388° N, 41.7197° E, on decayed wood of *Abies nordmaniana*, 7 Jun 2012, field, leg. Novozhilov Yu.K., Schnittler M. and Erastova D.A. (LE289730).

https://doi.org/10.48130/mycosphere-0026-0012

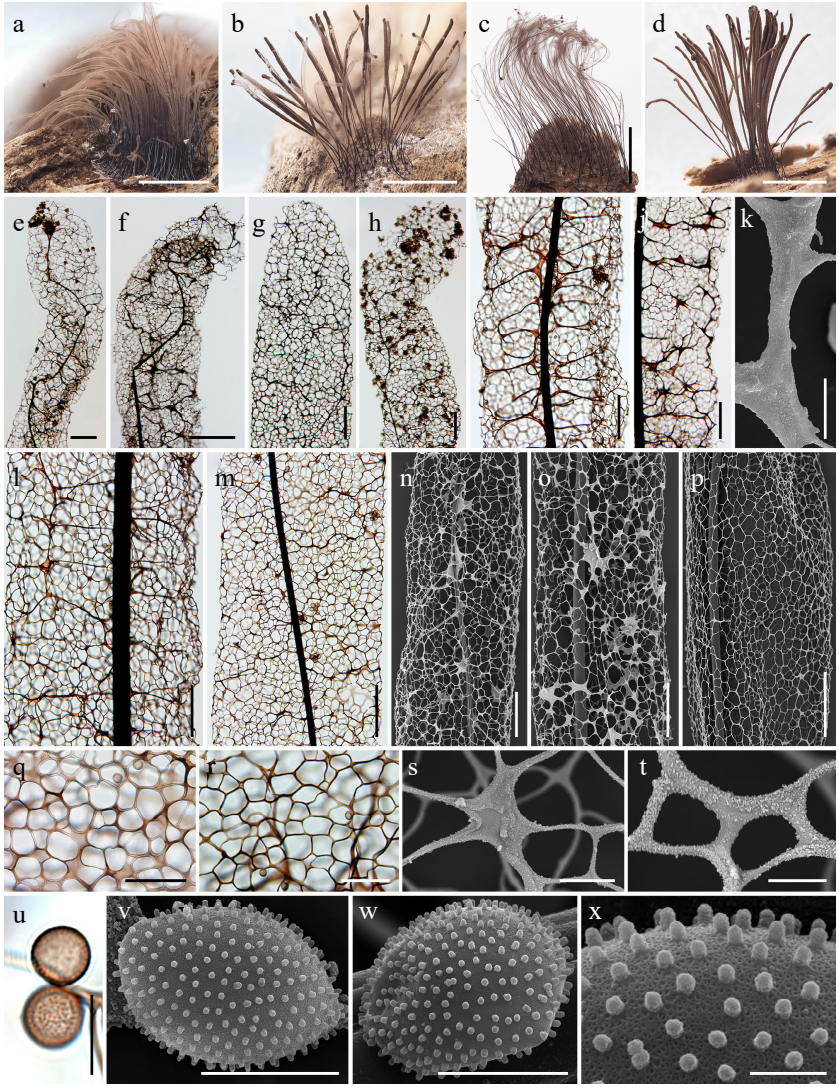

Fig. 42 Morphological characteristics of *Symphytocarpus splendens* (a), (p) HFNNU 13261; (b) HFNNU 10977; (c) HMAS 74774; (d) HFNNU 10990; (e), (l) HMAS 72488; (f) HMAS 78091; (g) HMAS 0294767; (h) HMAS 72518; (i) HFNNU 12500; (j) HMAS 0295162; (k), (w) MYX 25029; (m) HMAS 0295149; (n)–(o) HMAS 0294776; (q) HMAS 0294767; (r) HMAS 0295150; (s)–(t) HFNNU 10977; (u) HMAS 0258263; (v), (x) MYX 19746. (a)–(d) Mature sporocarps (DM). (e)–(h) Apical region of the sporocarp (LM). (i), (j) Capillitium in the middle part of the sporotheca (LM). (k) Detail of the capillitium threads (SEM). (l), (m) Capillitium in the middle part of the sporotheca (LM). (n)–(p) Surface net (SEM). (q), (r) Detail of the surface net (LM). (s), (t) Detail of the surface net (SEM). (u) Spores (LM). (v), (w) Spore (SEM). (x) Detail of the spore ornamentation (SEM). Scale bars: (a)–(d) = 3 mm; (e)–(j), (l)–(p) = 100 μm; (q), (r) = 10 μm; (k), (s), (u) = 10 μm; (t), (v), (w) = 5 μm; (x) = 1 μm.

Distribution: currently known from European Russia (Karachayevo-Circassian Republic).

Habitat: on rotten wood.

Notes: *Symphytocarpus tenuipes* is highly similar in gross morphology to *Sym. splendens*. Detailed comparison, however, reveals stable differences. The surface net threads of *Sym. tenuipes* (Fig. 43h, k, l–n) are noticeably more delicate and fragile than those of *Sym. splendens* (Fig. 42m–t), resulting in a more fragile net overall. More importantly, the two differ in spore ornamentation. The spores of *Sym. tenuipes* bear nearly uniformly distributed bacula and a surface with only sparse, flattened warts, not forming a dense reticulum (Fig. 43o–r). In contrast, spores of *Sym. splendens* (Fig. 42u–x) have denser and longer bacula, and the entire surface is covered with dense, pore-like structures that form a dense reticulum[71,73].

Stemonitis sichuanensis is also similar in sharing comparable sporocarp size and a columella that often expands at the sporotheca apex[113]. It differs in its shorter stalk (13%–17% of the total height), smaller spores (6–7 μm in diameter), and a spore ornamentation where the warts are interconnected at the base by a fine dense reticulum. *Stemonitis lignicola* Nann.-Bremek. (treated as a synonym of *Sym. splendens* by some) has a relatively dense capillitium[134] but lacks an apical columellar expansion; its fine-meshed surface net and normally developed internal capillitium differ from those of *Sym. splendens*[134], suggesting its synonymy requires more careful examination, particularly of spore ornamentation.

Phylogenetically, *Sym. tenuipes* forms a well-supported clade sister to *Sym. minor* (UBS/PP/TBE = 100/100/100; Fig. 1), from which it is morphologically distinct (see above). Based on its unique combination of morphological characteristics, coupled with its independent phylogenetic position, it is recognized as a new species.

***Symphytocarpus uniforatus* W.L. Song & Shuang L. Chen, sp. nov.**
Fig. 44

MycoBank number: MB863126.

Etymology: *uniforatus* (Latin) possessing uniform holes or pores, from *unus* (one, single, same) and *foratus* (pierced, bored, having

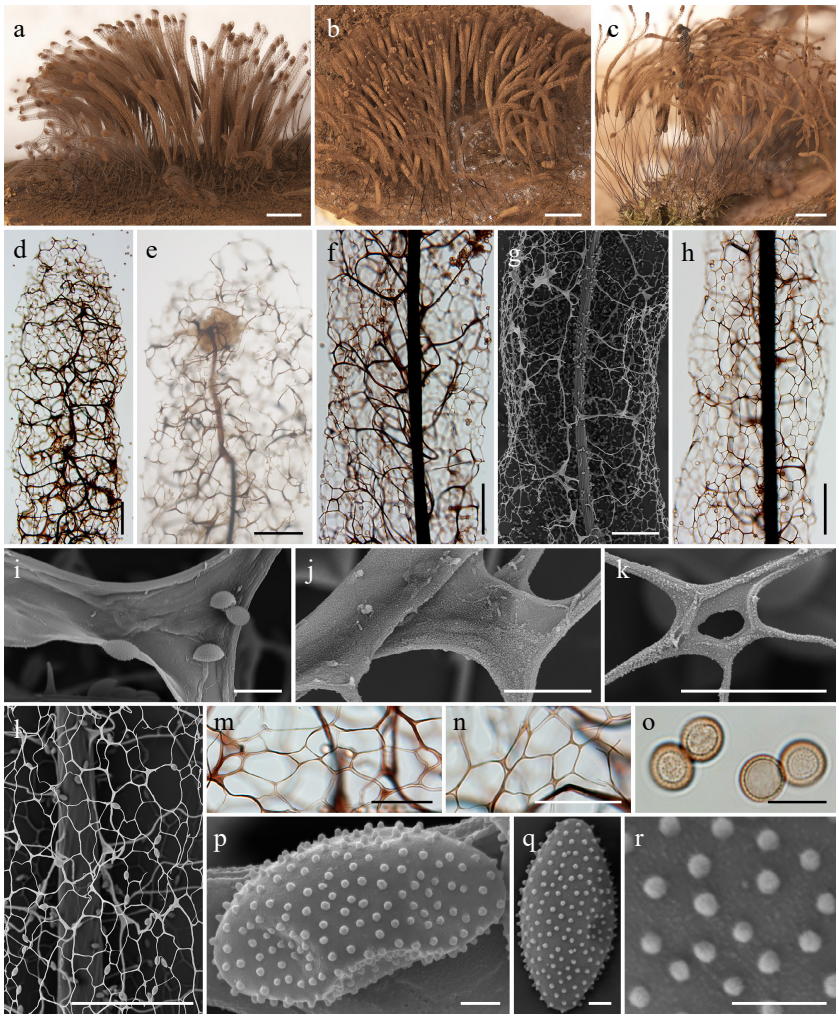

Fig. 43 Morphological characteristics of *Symphytocarpus tenuipes* (a), (f), (h), (j), (l), (q), (r) LE289704; (b), (e), (p) LE289716; (c) LE289730; (d), (g), (i), (k), (m)–(o). LE285125. (a)–(c) Mature sporocarps (DM). (d), (e) Apical region of the sporotheca (LM). (f) Capillitium in the middle part of the sporotheca (LM). (g) Capillitium in the middle part of the sporotheca (SEM). (h) Surface net (LM). (i), (j) Detail of the capillitium threads (SEM). (k), (l) Detail of the surface net (SEM). (m), (n) Detail of the surface net (LM). (o) Spores (LM). (p), (q) Spore (SEM). (r) Detail of the spore ornamentation (SEM). Scale bars: (a)–(c) = 2 mm; (d)–(h), l = 100 μm; (m), (n) = 10 μm; (i)–(k), (o) = 10 μm; (p)–(r) = 1 μm.

holes), referring to the surface net whose meshes are even and similar in size throughout the sporotheca.

Holotype: CHINA, Jiangxi Province, Yichun City, Mingyue Mountain National Forest Park, 20.6300° N, 114.3200° E, on rotten wood, 16 Jul 2022, field, leg. Chen S.L. and Yan S.Z. (HFNNU 4214, GenBank *nrSSU*: PZ106599; *mtSSU*: PX940091).

Diagnosis: Sporocarps measuring (6.8–)7.1–7.8(–8.1) mm in total height; stalk short, (1.1–)1.6–1.8(–2.2) mm long; surface net with uniformly sized meshes, (2.7–)10.5–15.7(–21.0) μm in diameter, lacking spines; spore (5.8–)6.4–6.9(–7.5) μm in diameter, ornamented with uniformly distributed bacula, with barely visible secondary ornamentation.

Description: Sporocarps erect, stalked, densely gregarious, (6.8–)7.1–7.8(–8.1) mm in total height. Sporotheca elongate-cylindrical, apex bluntly rounded, deep orange to brown, 0.2–0.3 mm wide. Stalk black, shiny, (1.1–)1.6–1.8(–2.2) mm long, 15%–30% of the total height, base forming a short cone. Hypothallus membranous, silvery white to translucent, shiny, common to the colony. Peridium evanescent. Columella black, tapering upwards, reaching the sporotheca apex as a slender filament. Capillitium arising from the entire length of the columella, black to brownish-orange, with a large triangular membranous expansion at the point of origin; much and intricately branched, with prominent membranous expansions at the branching points, threads coarse, densely covered with small warts, connecting to the surface net. Surface net well-developed, often incomplete at the sporotheca apex but complete elsewhere, threads filamentous; meshes of approximately equal diameter, (3–)10–16(–21) μm, threads densely covered with irregular small warts, without spines. Spore concolorous with the sporotheca in mass, brown to brownish orange or lighter in transmitted light, globose to subglobose, (5.8–)6.4–6.9(–7.5) μm in diameter, ornamented with uniformly distributed bacula, without secondary ornamentation. Plasmodium not observed.

Additional materials examined: CHINA, Heilongjiang Province, Greater Khingan Range, Qixia Mountain Botanical Garden, 52.3519° N, 124.7051° E, on rotten wood, 30 Jul 2024, field, leg. Chen S.L. and Yan S.Z. (HFNNU 12194).

Distribution: currently known from Eastern and Northeastern China.

Habitat: on rotten wood.

Notes: One of the closest species is *Ste. lignicola*, which has clustered brown sporocarps with very short stalks within *Stemonitis* s.l., noticeable expansions in the internal net, and spores with secondary ornamentation that is almost indistinguishable or even

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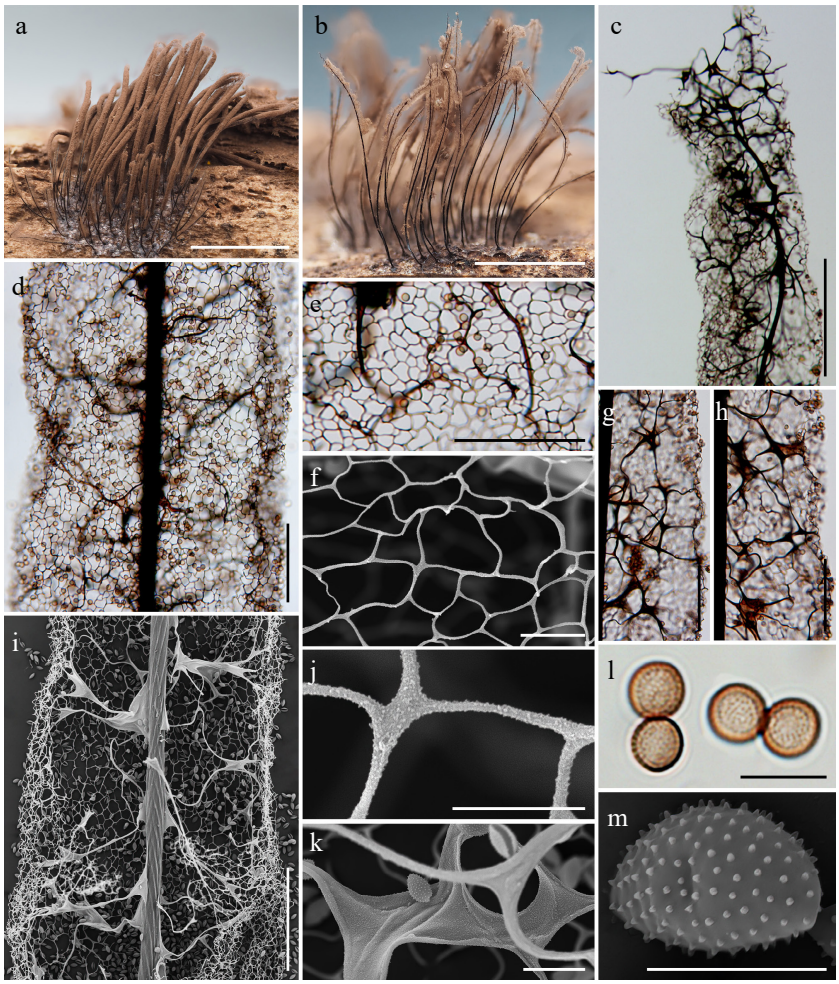

Fig. 44 Morphological characteristics of *Symphytocarpus uniforatus* (a), (c), (f)–(m) HFNNU 4214; (b), (d), (e) HFNNU 12194. (a), (b) Mature sporocarps (DM). (c) Apical view of the sporotheca (LM). (d) Surface net (LM). (e) Detail of the surface net (LM). (f) Detail of the surface net (SEM). (g), (h) Capillitium in the middle part of the sporotheca (LM). (i) Capillitium in the middle part of the sporotheca (SEM). (j) Detail of the surface net (SEM). (k) Detail of the capillitium threads (SEM). (l) Spores (LM). (m) Spore (SEM). Scale bars: (a), (b) = 3 mm; (c) = 200 μm; (d), (e), (g)–(i) = 100 μm; (f), (k), (l) = 10 μm; (j), (m) = 5 μm.

absent under SEM[77,134]. However, *Ste. lignicola* can be distinguished by its larger sporocarps (mostly 9–13 mm), larger capillitial meshes (8–40 μm), and slightly larger spores: 7–8 μm vs 5.8–7.5 μm. Nevertheless, due to the lack of molecular data for the more typical *Ste. lignicola*, the distinction between these species should be treated with caution.

Symphytocarpus uniforatus is morphologically also similar to *Cor. pallida*[83] but a series of stable differences exists. The sporocarps of *Sym. uniforatus* are taller [(6.8–)7.1–7.8(–8.1) mm vs 5–6 mm in the *Cor. pallida* syntype; Moreno et al.[71] and have a shorter stalk [(1.1–)1.6–1.8(–2.2) mm vs 2–2.5 mm]. More importantly, *Sym. uniforatus* possesses a well-developed surface net whose threads are distinct and completely lack spines (Fig. 44d–f, j), contrasting with the delicate, pale, and spiny surface net of *Cor. pallida*[71]. *Symphytocarpus uniforatus* also shows some resemblance to *Sym. ferrugineus*[71,124] in having a capillitium with membranous expansions and a surface net that lacks or bears very few spines. However, the two are readily separated by spore ornamentation: *Sym. ferrugineus* has spores almost smooth in LM with scarce, thick, short bacula overlaid by a dense, delicate reticulum in SEM[71], whereas *Sym. uniforatus* has spores distinctly warted in LM and with nearly uniformly distributed bacula and barely visible secondary ornamentation in SEM. Furthermore, the capillitium of *Sym. uniforatus* is sparser, and the membranous expansions at its branching points are more abundant and irregular in shape (Fig. 44g–i).

Phylogenetically, *Sym. uniforatus* forms an independent, well-supported clade (UBS/PP/TBE = 100/100/100; Fig. 1) within *Symphytocarpus* and is not sister to any other known or newly described species. Based on its combination of stable morphological distinctions and its distinct phylogenetic position, it is confirmed as a new species.

Discussion

Data limitations and phylogenetic resolution

Stemonitidales currently comprises two families and 11 genera[135]. The family Amaurochaetaceae includes *Brefeldia* Rostaf., *Enerthenema*, *Macbrideola*, *Comatricha*, *Paradiacheopsis*, and *Amaurochaete*, whereas Stemonitidaceae contains *Valtocarpus*, *Symphytocarpus*, *Stemonaria*, *Stemonitis*, and *Stemonitopsis*. This study focuses primarily on the genera of Stemonitidaceae but also includes *Amaurochaete*. Drawing upon comprehensive sampling from Belarus (27), Brazil (two), China (94), Japan (10), Nepal (two), Russia (151, including one from Russian Empire), the USA (one), and Vietnam (three), the most extensive phylogeny of Stemonitidales to date, was constructed utilizing three gene fragments: *nrSSU*, *EF-1α*, and *mtSSU*. The results support previous findings of phylogenetic stability within the order[19,27,88] and corroborate the reliability of

certain intergeneric relationships. Similar to recent large-scale taxonomic revisions in other complex lineages[136], this multi-gene approach underscores the critical role of integrative morpho-molecular analyses in resolving long-standing taxonomic confusion and establishing robust generic boundaries.

Despite its expanded taxon sampling, the phylogenetic tree generated in this study reveals certain data limitations. A notable limitation is the geographic bias in specimen representation. Although numerous species of Stemonitidaceae are distributed in tropical, Neotropical, and subtropical regions[82,107,126,137,138], the current dataset is predominantly concentrated in temperate and subtropical Eurasia (Supplementary Table S1). This uneven geographic sampling limits the comprehensiveness of a global taxonomic revision, as the phylogenetic diversity of tropical and subtropical lineages remains underrepresented. Furthermore, DNA sequence data are currently lacking for type or recently collected specimens of several species, such as *Stp. peritricha*, *Ste. capillitionodosa*, *Ste. sichuanensis*, *Ste. virginiensis*, and *Ste. uvifera*. Additionally, detailed morphological examinations were conducted on the type materials of various known taxa, including *Sta. argentella* (Fig. 9), *Sta. clausifila* (Fig. 10), *Sta. gracilis* (Fig. 21), *Sta. laxiretis* (Fig. 11), *Sta. minuta* (Fig. 24), *Sta. pallidofila* (Fig. 6), *Ste. emotoi* (Fig. 16), *Ste. laxifila* (Fig. 5), *Ste. marjana* (Fig. 23), *Ste. pallida* var. *rubescens* (Fig. 39), *Ste. splendens* (Figs 40, 41), *Stp. aequalis* var. *microspora* (Fig. 36), and *Stp. curiosa* (Fig. 14). However, successful DNA extraction and sequencing from these materials were not possible due to their considerable age or fungal contamination. These data gaps have, to some extent, limited the resolution and comprehensiveness of the phylogenetic inferences, highlighting the challenges of obtaining high-quality genetic data from historical or compromised specimens.

Despite these data gaps in the molecular analysis, the present study integrates the current phylogenetic framework with detailed morphological data to describe 13 new species. This further indicates that myxomycete taxa comply with the biological species concept[139–141]. Although the sample sizes for individual taxa in the present study preclude a formal population-level recombination analysis, the mutual exclusivity of the allele pools for all delineated species was verified across three independently inherited markers (*nrSSU*, *EF-1α*, and *mtSSU*). An examination of the single-gene phylogenies (Supplementary Figs S1–S3) revealed expected topological discordances compared to the concatenated tree, such as the lack of deep resolution in the short *EF-1α* exon alignment and the ambiguous topology of the *mtSSU* dataset driven by varying evolutionary rates and missing data. Nevertheless, the critical observation is that each recognized species possesses unique genetic variants for the studied markers. No instances were found where two distinct species shared a 100% identical sequence for any of the three loci. The strict uniqueness of ribotypes and genotypes for each designated taxon demonstrates the mutual exclusivity of their allele pools, thereby providing robust molecular validation for the narrow species concept applied to the taxa in this study.

In addition, this study resurrects two previously synonymized species (*Ste. castillensis* and *Ste. emotoi*), reinstates three basionyms to replace currently accepted combinations, and proposes 29 new combinations alongside one replacement name. Among these 29 new combinations and the one replacement name (Supplementary Table S3), six combinations are supported by morphological characteristics and unambiguous molecular evidence, whereas 23 combinations and one replacement name are inferred solely from morphological analyses. These morphological inferences are founded on detailed original descriptions and high-quality illustrations (e.g., *Cor. capillitionodosa*, *Cor. gracilis*, *Cor. mediterraneensis*, *G. smithii*, *Ste. liaoningensis*, *Ste. longoides*, *Ste. pilosa*, *Ste. reticulospora*, *Stp. meandrispora*, *Stp. orthotricha*, *Stp. subalpina*, *Sym. planus*, *Sym. rhizoideipes*, and *Sym. sichuanensis*), recent high-quality SEM studies of type materials (e.g., *Cor. flavogenita*, *Cor. pallida*, *Cor. pulchella*, and *Ste. pseudonigra*), or re-examinations of type materials conducted in this study (e.g., *Cor. laxifila*, *Cor. pallidofila*, *Ste. curiosa*, *Ste. minuta*, *Sym. microsporus*, and *Sym. rubescens*). Relying exclusively on spore ornamentation characteristics, such as apically thickened pillars, for generic placement introduces a degree of phylogenetic uncertainty. Nevertheless, this approach is deemed necessary to maintain nomenclatural consistency and to prevent these taxa from becoming orphaned following the disbandment or redefinition of their original genera. To ensure transparency, these taxa are explicitly distinguished within the established taxonomic framework as morphological species pending future molecular confirmation. Future studies will require more geographically balanced specimen collection, particularly targeting tropical and subtropical ecosystems, optimized DNA extraction protocols, and the integration of multi-gene and genomic approaches[19] to test these morphology-based hypotheses and further refine the phylogenetic framework of Stemonitidales.

Generic boundaries and paraphyly of *Symphytocarpus*

In this study, the genera *Amaurochaete*, *Corallosporopsis*, *Grandiverruca*, *Stemonitis*, *Stemonitopsis*, and *Valtocarpus* are each recovered as monophyletic, whereas *Symphytocarpus* remains paraphyletic (Fig. 1). This pattern stems from two primary lines of evidence. First, several specimens tentatively assigned to *Symphytocarpus* based on morphology (e.g., LE325220, LE285115, MYX 25012, MSK-F 43596, etc.) do not cluster within its core monophyletic clade. Second, *Sym. dispersus* (Fig. 30), although morphologically consistent with *Symphytocarpus*, is phylogenetically placed as sister to the *Stp. hyperopta* agg. (type of *Stemonitopsis*) and falls outside the main *Symphytocarpus* lineage (Fig. 1). These results indicate that *Symphytocarpus* as currently circumscribed, primarily based on morphological characteristics such as spore ornamentation and color, may encompass multiple independent evolutionary lineages that could be recognized as distinct monophyletic genera in the future. Similar patterns have been reported in other myxomycete groups; for example, *Diacheopsis resinae* Woerly & Gøtzsche resolves into three highly supported clades in molecular phylogenies[142], and taxa historically placed in *Physarum* have recently been segregated into genera such as *Claustria*, *Aethaliopsis*, and *Nannengaella*[14] based on multi-gene phylogenies. Therefore, broader sampling within the *Symphytocarpus* complex, coupled with the identification of more stable morphological diagnostic characteristics beyond spore traits, is likely to refine the current paraphyletic structure and lead to a clearer taxonomic system.

Taxonomic significance of surface net and spore ornamentation

This study further confirms the limitations of traditional taxonomic approaches that rely predominantly on single, variable morphological characteristics such as completeness of the surface net and the presence of a fibrous structure at the base of the stalk. For instance, *Stemonaria* was established to accommodate species difficult to place elsewhere[24], *Stemonitopsis* was circumscribed for species with an incomplete surface net[23], and *Symphytocarpus* was created for taxa with an incomplete surface net, a short stalk, and aggregated sporocarps[23]. The structure of the stalk base (fibrous vs horny) was another cornerstone of this system, culminating in its use to separate the group into Stemonitidaceae and

Amaurochaetaceae[4]. However, the three-gene phylogeny presented here (Fig. 1) demonstrates that species with complete, incomplete, or even absent surface nets do not form corresponding monophyletic groups. Instead, species within Stemonitidales are primarily grouped into distinct evolutionary lineages based on spore characteristics and sporocarp morphology (habit). This suggests that, within Stemonitidaceae, specifically the *Stemonitis* s.l. complex, spore ornamentation and sporocarp morphology may convey more reliable phylogenetic signals than characteristics of the surface net.

The results of this study strongly support the view that spore ornamentation is among the most stable taxonomic characteristics for generic delimitation within Stemonitidaceae. Spore dispersal in nature is closely tied to these traits, which are strongly influenced by evolutionary processes and have proven to be robust indicators of deep phylogenetic relationships[143–145]. This is clearly illustrated by the phylogenetic clustering in this study. All taxa with spores bearing bacula that possess characteristically thickened apices (Fig. 45) form a distinct clade, such as *Cor. flavogenita*, *Cor. pallida*, *Cor.* cf. *gracilis* MYX 22279, and *Cor.* cf. *gracilis* LE348922, recognized here as *Corallosporopsis*, irrespective of other variable characteristics such as surface net condition and fibrous or horny structure of the stalk. Taxa with spores exhibiting a secondary ornamentation of varying prominence (Fig. 46), typically accompanied by a densely gregarious habit and orange-brown sporotheca, collectively comprise the redefined *Symphytocarpus*. While Rammeloo[36] classified spore ornamentation in Stemonitidales into eight basic types, this study proposes that the presence of apically thickened bacula (defining *Corallosporopsis*) and the presence or absence of a secondary ornamentation should be recognized as a distinct characteristic state with independent taxonomic value.

Most significantly, all species with spores ornamented by a simple reticulum of perforated muri (Fig. 47) form the well-supported *Stemonitis* s.str. clade (UBS/PP/TBE = 100/-/94; Fig. 1). This clade includes members with complete, incomplete, or absent surface nets, clearly demonstrating that surface net completeness is a plastic characteristic unsuitable as a primary generic criterion.

Slight variations within this ornamentation pattern, such as whether the pillars exceed the tops of the muri, their arrangement, and mesh density, provide key morphological criteria for distinguishing species within this group[71,100]. Within the simple-reticulate spore type that defines *Stemonitis* s.str., several finer structural subtypes can be identified based on SEM observations: 1) pillars distinctly surpassing the muri tops, represented by *Ste. spinimuralis* (Figs 39, 47t), *Ste. imperfecta* (Figs 22, 47m), and *Ste.* cf. *foliicola* (Figs 18, 47g); 2) pillars and bridges flattened and widened, with small perforations, and pillars not exceeding the bridge tops, represented by *Ste. amphorocolumella* (Fig. 47a), *Ste. castillensis* (Figs 12, 47b), *Ste. conferta* (Figs 13, 47c), and *Ste.* cf. *pilosa* (Figs 26, 47r); 3) pillars surpassing the muri tops, with bridges finer at their junctions with the pillar apices, represented by *Ste. emotoi* (Figs 16, 17, 47f), *Ste. curvicornis* (Figs 15, 47e), *Ste. pinnatiapicalis* (Figs 27, 47s), and *Ste.* aff. *fusca* (Figs 19, 47h); and 4) pillars not exceeding the bridge tops, represented by *Ste.* cf. *pinicola*, *Ste. amaurochaetoides* (Fig. 47a), *Ste. longa* (Fig. 47n), and *Ste. fusca* agg. (Figs 20, 47i). These subtle variations may suggest the existence of further, morphologically recognizable subgroups within *Stemonitis* s.str., highlighting the high diagnostic value of spore ultrastructure. However, given the limited material in the current study, it would be premature to draw definitive taxonomic conclusions based on these patterns alone. Expanded sampling and detailed comparative SEM studies are required to validate the consistency and taxonomic significance of these fine-scale characteristics.

Furthermore, the critical reliance on spore ornamentation for taxonomy underscores the necessity for high-quality imaging standards. The findings of this study are contingent on the detailed visualization of spore surfaces using SEM. It is essential to note that the interpretative value of such characteristics depends heavily on the resolution and magnification of the micrographs. Consequently, future studies should aim to document spore ornamentation, especially of type specimens, at the highest practical magnification. Published SEM images taken at low magnification or with technically limited equipment[67,82,113,146,147] can be of limited diagnostic use and may obscure taxonomically significant microstructures.

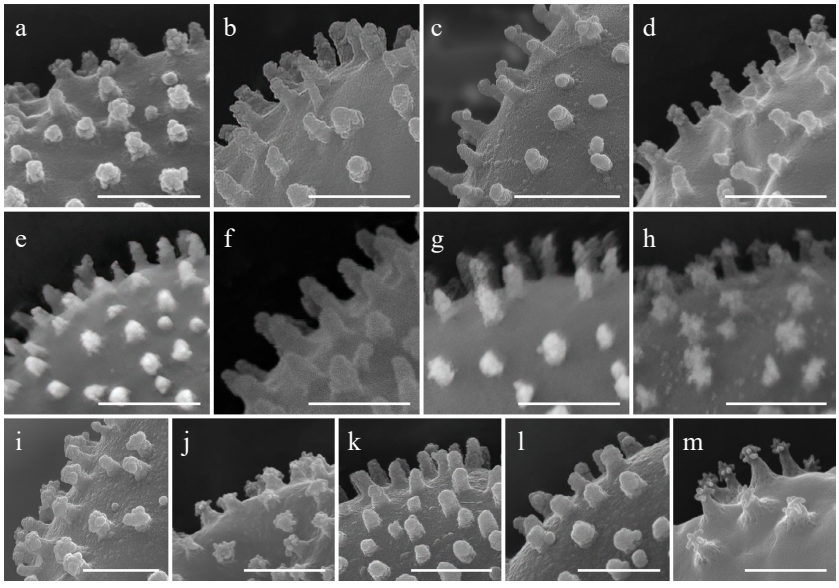

Fig. 45 Comparison of spore ornamentation among *Corallosporopsis* species involved in this study. (a) *Corallosporopsis flavogenita* LE325169. (b) *Corallosporopsis flavogenita* LE325481. (c) *Corallosporopsis* cf. *gracilis* MYX 22279. (d) *Corallosporopsis* cf. *gracilis* LE348922. (e) *Corallosporopsis* cf. *herbatica* HMAS 98461. (f) *Corallosporopsis* cf. *herbatica* LE348810. (g) *Corallosporopsis laxifila* TNS-M-H-4376. (h) *Corallosporopsis pallidofila* TNS-M-Y-22050. (i) *Corallosporopsis gabrieliana* LE306548. (j) *Corallosporopsis gabrieliana* LE306833. (k) *Stemonitopsis* cf. *aequalis* MYX 15509. (l) *Corallosporopsis* sp. LE325737. (m) *Corallosporopsis spinispora* LE297432. Scale bars: 1 μm.

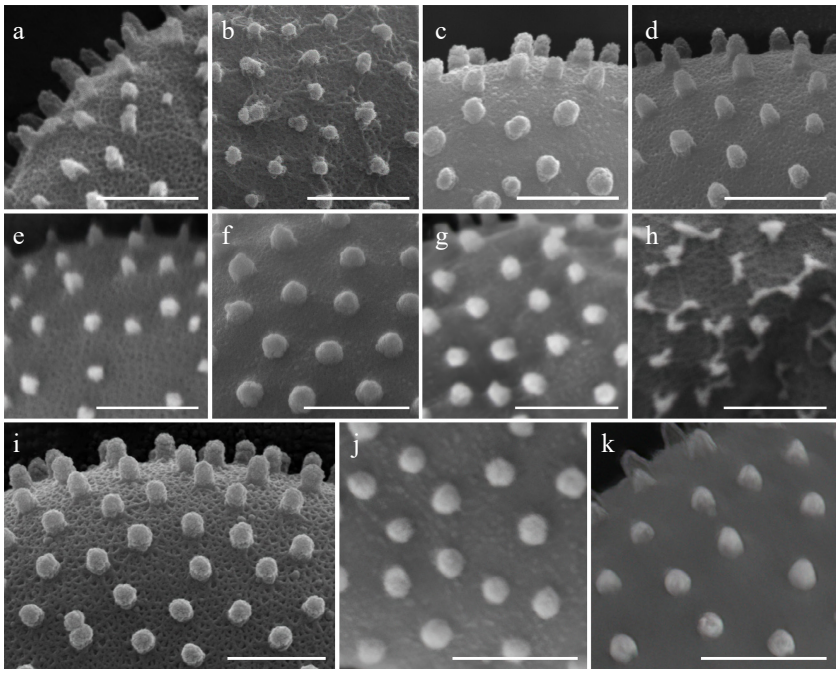

Fig. 46 Comparison of spore ornamentation among *Symphytocarpus* species involved in this study. (a) *Symphytocarpus dispersus* LE352558. (b) *Symphytocarpus ferrugineus* MYX 19217. (c) *Symphytocarpus laxicarpicus* MYX 23608. (d) *Symphytocarpus flaccidus* LE47610. (e) *Symphytocarpus microsporus* TNS-M-Y 22052. (f) *Symphytocarpus minor* LE348776. (g) *Symphytocarpus pseudoflavogenitus* HFNNU 11433. (h) *Symphytocarpus rubescens* TNS-M-Y 22055. (i) *Symphytocarpus splendens* MYX19796. (j) *Symphytocarpus tenuipes* LE289704. (k) *Symphytocarpus uniforatus* HFNNU4214. Scale bars: 1 μm.

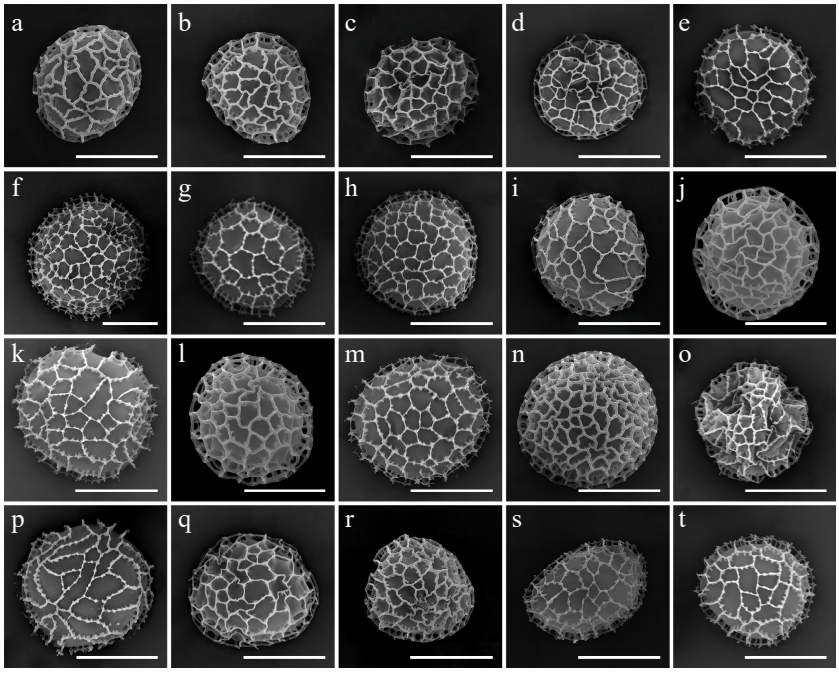

Fig. 47 Comparison of spore ornamentation among *Stemonitis* s.str. species involved in this study. (a) *Stemonitis amaurochaetoides* MYX 7126. (b) *Stemonitis castillensis* LE286562. (c) *Stemonitis conferta* HFNNU 8578. (d) *Stemonitis curiosa* TNS-M-Y-22056. (e) *Stemonitis curvicornis* HFNNU 10969. (f) *Stemonitis emotoi* HFNNU 10802. (g) *Stemonitis* cf. *foliicola* MSK-F 43589. (h) *Stemonitis* aff. *fusca* MSK-F 43584. (i) *Stemonitis fusca* agg. MYX 19459. (j) *Stemonitis fuscoides* MYX 12516. (k) *Stemonitis gracilis* TNS-M-Y-22046. (l) *Stemonitis* cf. *gracilis* MYX 10257. (m) *Stemonitis imperfecta* HFNNU 8808. (n) *Stemonitis longa* MYX 24803. (o) *Stemonitis marjana* TNS-M-Y-22054. (p) *Stemonitis minuta* TNS-M-Y-22049. (q) *Stemonitis palustris* LE346780. (r) *Stemonitis* cf. *pilosa* MYX 24418. (s) *Stemonitis pinnatiapicalis* LE325372. (t) *Stemonitis spinimuralis* HMAS 0257700. Scale bars: 5 μm.

Establishing a common standard, for instance, imaging spores at magnifications sufficient to clearly resolve the fine details of bacula, reticulum, and perforations, will greatly enhance the comparability and long-term utility of morphological data in the systematics of Stemonitidales and other myxomycete groups.

However, it is important to note that this finding cannot yet be generalized across all myxomycete groups. For instance, in *Meriderma*, a single monophyletic lineage can exhibit a wide spectrum of spore ornamentation patterns, ranging from reticulate to baculate[18,35].

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Diagnostic value of spore size

Based on the available data, spore diameter shows potential diagnostic value primarily at the generic level, as the size ranges often differ among clades and can serve as a supplementary delimiting characteristic. However, at the species level, particularly among closely related taxa, relying solely on spore size for distinction is often unreliable. In *Grandiverruca*, all species possess spores not exceeding 6 μm, with extensive overlap between species, rendering spore size of limited value for intrageneric discrimination (Fig. 48). *Corallosporopsis* exhibits a broader spore-diameter range (6.0–11.9 μm), with most species concentrated between 9–10 μm. Within this genus, *Cor. pallidofila* has the largest spores, whereas *Cor. pulchella* and *Cor. pallida* possess smaller spores (6–8 μm) with nearly overlapping size ranges. In *Symphytocarpus*, spore diameters range from 4.8 to 10 μm, with most species falling between 6–8 μm; *Sym. planus* and *Sym. rhizoideipes* reach the upper limit of the genus (10 μm). Although spore size does not clearly separate *Sym. dispersus* from *Sym. ferrugineus*, or *Sym. minor* from *Sym. uniforatus*, it may still provide useful information for distinguishing other species in the genus. *Stemonitis* displays the widest variation in spore diameter (5.5–13.1 μm). Notably, *Ste. emotoi* possesses the distinctly largest spores within the genus; measurements of fresh material in this study show a diameter of (11.0–)11.7–12.6(–13.1) μm, while its holotype measures (10.2–)10.9–12.0(–12.5) μm. The lower limit of spore size in *Ste. emotoi* almost overlaps with the upper limit of *Ste. amphorocolumella* (which reaches up to 11 μm). In contrast, species such as *Ste. longa*, *Ste. longoides*, *Ste. pseudonigra*, and *Ste. virginiensis* have comparatively smaller spores (5.5–6.5 μm). In summary, spore diameter is an informative morphological characteristic that can aid generic delineation. However, minor fluctuations (e.g., up to ± 1 μm) are likely attributable to environmental plasticity, as has been similarly demonstrated in other myxomycetes such as *Badhamia albescens* (Ellis ex T. Macbr.) J.M. García-Martín, J.C. Zamora & Lado[148]. Therefore, due to intraspecific variation and

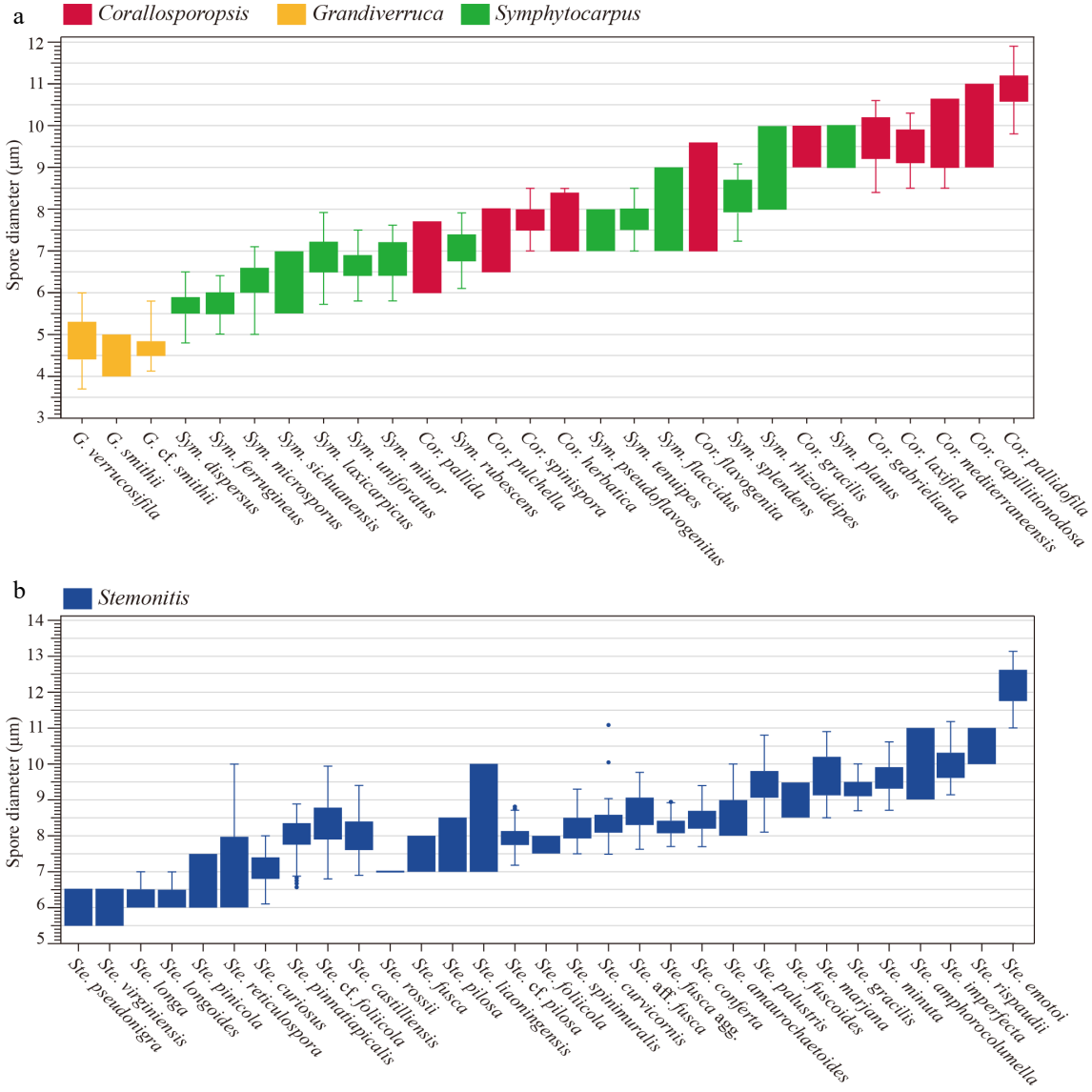

Fig. 48 Comparative analysis of spore diameters. (a) Warted-spore species belonging to *Corallosporopsis* (red), *Grandiverruca* (yellow) and *Symphytocarpus* (green). (b) Reticulate-spore species of *Stemonitis* (blue). Only species assigned to categories A (Accepted species) and categories B (Morphospecies included but not yet phylogenetically studied) in the taxonomic framework of this study are included; category C species are excluded. Within each panel, species are arranged left-to-right in order of increasing minimum spore diameter; when minima are equal, the order is based on increasing maximum diameter; if both minima and maxima coincide, species are listed alphabetically. Data from specimens examined in this study (including re-examined type material) or original descriptions for species not directly studied.

frequent interspecific overlap, it should be integrated with other characteristics, such as spore ornamentation, sporocarp structure, ecological data, and molecular evidence, to improve the accuracy of taxonomic determinations.

Reliability of sporotheca color

The color of the spore mass (sporotheca) may hold some taxonomic value as a morphological characteristic. In this study, distinctions among genera were observed: members of *Stemonitis* typically have dark brown sporotheca; members of *Symphytocarpus* and *Grandiverruca* typically have brown sporotheca with varying orange tints, whereas the *Stp. hyperopta* agg. exhibits a characteristic violet or pinkish hue (Fig. 49). *Corallosporopsis* shows the greatest variation, ranging from pale to dark brown and rarely orange brown. Within a given species, sporotheca color appears to be a stable characteristic. For example, specimens of *G.* cf. *smithii* from European and Far Eastern Russia (separated by more than 6,500 km) are nearly identical in color, as are those of *Cor. gabrieliana*, *Sym. dispersus*, and *Sym. minor* (Fig. 37). Color can also help distinguish some species; for instance, *Sym. minor* is noticeably darker than *Sym. ferrugineus* and slightly darker than *Sym. laxicarpicus* and *Sym. uniforatus*. However, this characteristic should be used cautiously for distinguishing closely related species, such as the many dark-brown taxa within *Stemonitis*. Sporotheca color can fade in older specimens, a phenomenon documented in genera like *Lycogala*[32,33] and *Arcyria*[34]. This effect appears less pronounced in Stemonitidales; for example, specimens collected in the 1980s and 1990s examined in this study retain their coloration well (Fig. 6 for *Cor. pallidofila*; Fig. 11 for *Sta. laxiretis*; Fig. 38 for *Sym. microsporus*; and Fig. 39 for *Sym. rubescens*). Similarly, in *Sym. ferrugineus*, little difference is evident between material collected from 1998 to 2024 (Supplementary Fig. S6). Nevertheless, the diagnostic utility of this trait is lost once the spores have dispersed.

Plasticity of sporocarp and columella morphology

In myxomycete taxonomy, sporocarp macromorphology (e.g., whether it is an aethalium or pseudoaethalium) has long been used as an important diagnostic characteristic. However, accumulating evidence indicates that sporocarp type alone is insufficient for distinguishing genera[149]. Analysis of the relevant taxa in this study reinforces this view and underscores the phylogenetic unreliability of using the pseudoaethalium characteristic as a primary diagnostic characteristic for *Symphytocarpus*[22]. The formation of pseudoaethalia, and even aethalia, may result from localized evolutionary events or developmental variations rather than reflecting common ancestry. This is evident in *Ste. amaurochaetoides*, the newly described *Ste. conferta*, and members of the monophyletic *Amaurochaete*, which, despite sharing similar aggregated sporocarps, are phylogenetically distant (Fig. 1). This plasticity reflects a broader pattern in myxomycetes, where similar macro-morphologies arise independently through convergent evolution[14,15,149]. Similar transitions towards aggregated sporocarps are widely observed in other major clades of myxomycetes, such as *Didymium spongiosum* (Leyss.) J.M. García-Martín, J.C. Zamora & Lado[150], *Didymium yulii*

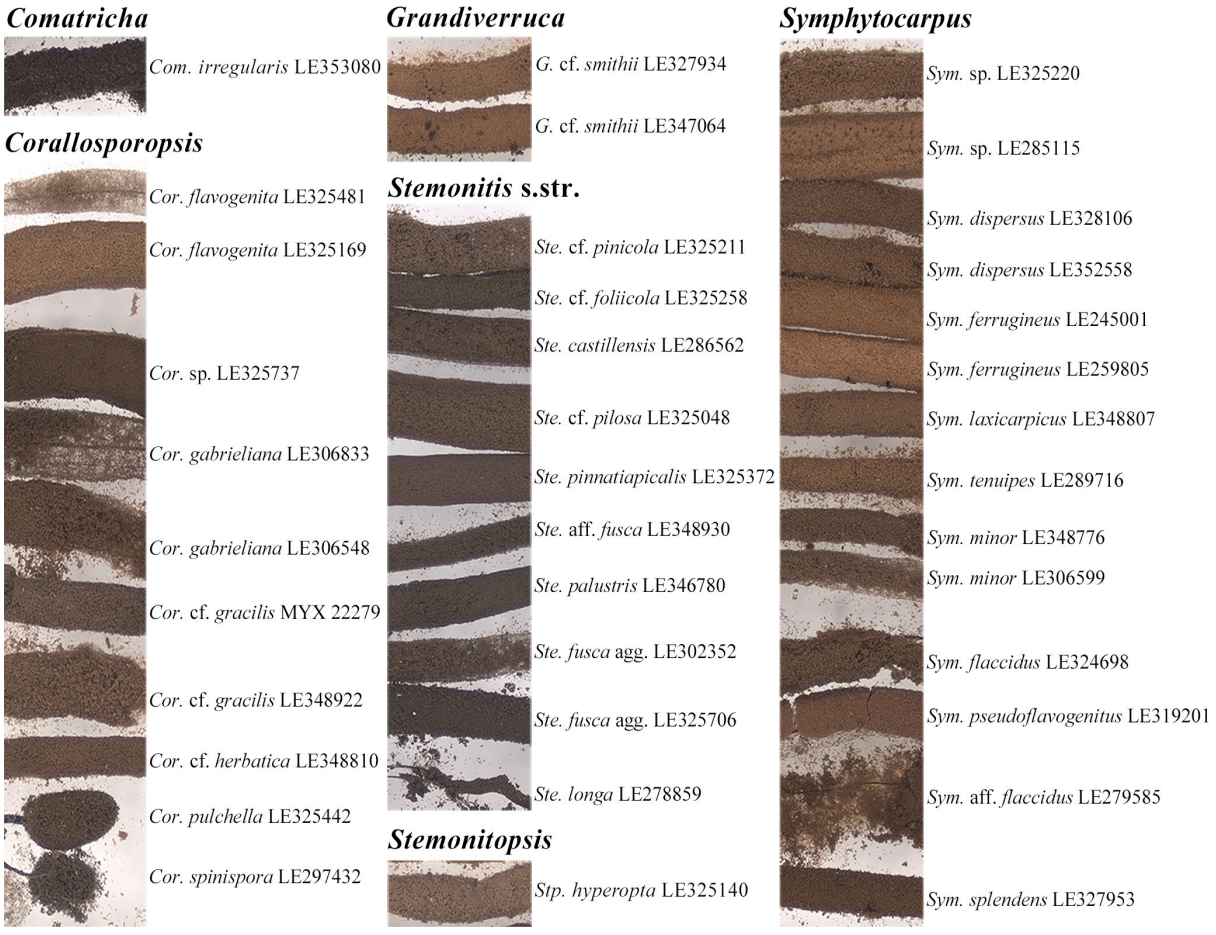

Fig. 49 Comparison of spore mass (sporotheca) coloration under standardized conditions for representative specimens of the genera *Comatricha*, *Corallosporopsis*, *Grandiverruca*, *Stemonitis* s.str., *Stemonitopsis*, and *Symphytocarpus*.

S.Y. Liu & F.Y. Zhao[151], and *Nannengaella laevis* (Pers.) J.M. García-Martín, J.C. Zamora & Lado (≡ *Fuligo laevis* Pers.)[14] within Columellomycetidae, and members of the Reticulariaceae[149] within Lucisporomycetidae.

In some species, such as *G. verrucosifila* (Fig. 8), *Ste. imperfecta* (Fig. 22), *Ste. marjana* (Fig. 23), and *Sym. microsporus* (Fig. 36), the overall sporocarp morphology is relatively constant. In others, particularly within *Symphytocarpus* (e.g., *Sym. splendens*, *Sym. ferrugineus*, *Sym. pseudoflavogenitus*), it shows considerable plasticity, sometimes even within a single collection (Fig. 50). While small sporocarp size (ca. 2–6 mm in total height) might seem characteristic of *Grandiverruca*, similarly small or even smaller sporocarps occur in other genera, such as *Ste. minuta* ([1.1–]1.2–1.6[–1.8] mm in total height) and *Sym. dispersus* ([1.8–]2.4–3.2[–3.9] mm in total height),

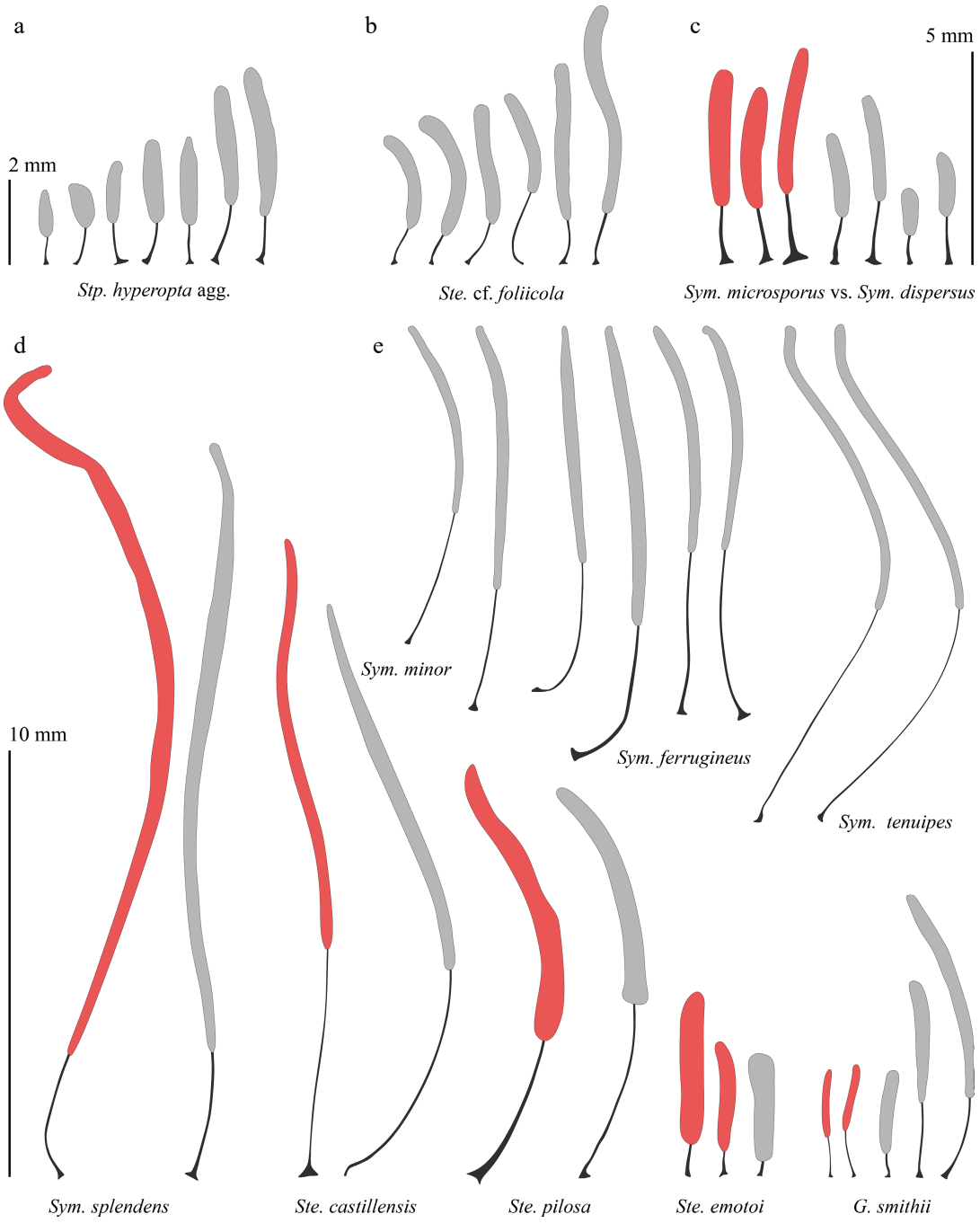

Fig. 50 Silhouettes of some of the discussed species on the same scale. The type specimens are highlighted in red. (a) Variations in the *Stemonitopsis hyperopta* species complex (LE229360, LE279778, LE325006, LE325108, LE325140, LE353078, mixed). (b) Variations in the species *Stemonitis* cf. *foliicola* (LE325205, LE325258, LE348878, mixed). (c) Comparison of related species *Symphytocarpus microsporus* and *Sym. dispersus* (TNS-M-Y-22052 [2 pcs.], type from Fig. 20b of Nannenga-Bremekamp & Yamamoto[99], LE348844, LE328106, LE327886, LE352558, from left to right). (d) Comparison of some studied specimens with the types of the corresponding taxa: *Sym. splendens* (LE46378 and LE327953), *Ste. castillensis* (type from Macbride [1893], Plate X, Fig. 5, and LE286564), *Ste. pilosa* (type from Nannenga-Bremekamp et al. [1984], Fig. 2b and LE325048), *Ste. emotoi* (TNS-M-Y-22053, type from Nannenga-Bremekamp et al., (1984), Fig. 7, HFNNU10801), *Grandiverruca smithii* (type from Macbride [1893], Plate X, Fig. 4, LE327934 [2 pcs.], LE347064). Everything is from left to right. (e) Comparison of similar species *Sym. minor*, *Sym. ferrugineus* and *Sym. tenuipes* (LE348772 [2 pcs.], LE245001 [2 pcs.], LE328110 [2 pcs.], LE289730 [2 pcs.]). Everything is from left to right.

further illustrating the instability of this macromorphological characteristic for generic distinction.

Consequently, relying on sporocarp type for generic delimitation can obscure true phylogenetic relationships, potentially creating artificial paraphyletic or polyphyletic groupings. Nevertheless, detailed documentation of sporocarp morphology retains significant practical value for species-level taxonomy. While direct comparison of outlines is impractical for routine identification, high-quality habit photographs and/or schematic drawings are invaluable (Fig. 50). They capture characteristics difficult to describe verbally and allow for intuitive comparison when microscopic characteristics are very similar, as between *Sym. splendens* and *Sym. tenuipes* (Fig. 50). When combined with quantitative data like spore-size boxplots, such imagery can serve as a graphical multi-access key, providing a powerful tool for species recognition and diagnosis.

Columella apex morphology (e.g., funnel-like, membranous, or thickened) is inconsistent and unreliable for taxonomy. Although used to delimit species like *Sym. pseudoflavogenitus*[69], *Cor. flavogenita*[13], *Cor. capillitionodosa*[13], and *Sym. sichuanensis*[113], this characteristic is highly variable. It is also present in the newly described *Sym. tenuipes* (Fig. 43). In this species, it varies from a distinct membranous expansion to a slight local thickening. Variation is even more pronounced in *Sym. pseudoflavogenitus*, where it can differ between sporocarps in the same collection or be entirely absent (Fig. 38d–h, i). Similar variability was observed in a few *Sym. splendens* specimens (Fig. 42e–h). In contrast, a distinct apical curvature may be more stable, as seen in *Ste. virginiensis*[71,100] and the new species, *Ste. curvicornis* (Fig. 15c, g) and *Ste. palustris* (Fig. 25c, d). Consequently, columella apex morphology is unsuitable as a sole unambiguous species-level diagnostic characteristic.

Taxonomic implications at the family level

The incongruent distribution of generic lineages within the current phylogenetic tree raises important questions regarding the higher-level classification of Stemonitidales. The family-level classification proposed by Leontyev et al.[4] recognized Amaurochaetaceae and Stemonitidaceae as distinct entities based primarily on stalk structure, specifically differentiating a fibrous stalk base from a horny stalk structure. Under this classification, *Stemonaria* and *Stemonitopsis* were assigned to Amaurochaetaceae due to the fibrous nature of their stalk bases[4]. However, Shchepin et al.[88] demonstrated that *Stp. typhina* resolves independently of these groups, forming a basal branch within the dark-spored myxomycete clade, and was subsequently accommodated in the new genus *Argentoderma*. Furthermore, the multi-gene phylogeny generated in the present study (Fig. 1) demonstrates that generic delimitation based on stable spore ornamentation characteristics does not align with the traditional separation based on stalk types. For instance, *Stp. hyperopta*, the type species of *Stemonitopsis*, is nested within Stemonitidaceae in the current topology. Lineages characterized by distinct spore ultrastructure often cluster independently of their stalk morphology, as exemplified by the grouping of all warted-reticulate-spored species into *Stemonitis* s.str. This incongruence suggests that the fibrous or horny nature of the stalk may represent a homoplasious trait resulting from convergent evolution under similar environmental pressures. Consequently, relying strictly on stalk structural characteristics to maintain the current dual-family scheme appears insufficiently supported by molecular and ultrastructural data. Although a formal taxonomic revision at the family level within Stemonitidales is deferred until genomic data, more geographically diverse specimens, and further historical type information are available to provide robust support for the deepest nodes of the order, the current results indicate that a revised family-level taxonomic scheme based on stable characteristic complexes, rather than solitary stalk characteristics, may be necessary to achieve a monophyletic higher-level classification.

Importance of type specimens and future directions

This study reiterates the fundamental importance of type specimens in taxonomy[71,152], regardless of their current taxonomic status. Direct examination of type material is essential for accurate identification, as exemplified by *Ste.* cf. *foliicola* in this study (Fig. 18) and *Badhamia ovispora* Racib.[153,154]. This underscores the foundational value of Moreno et al.'s work[59,71,73,78]. However, a substantial portion of the pertinent type specimens were not accessible for that research. Given the requirements of modern taxonomy, systematically examining all available type specimens in herbaria worldwide has become a crucial task[65,98,155–157]. Priority should be given to the herbarium of N.E. Nannenga-Bremekamp and the personal collection of B. Ing, which contain numerous Stemonitidales species, including *Sym. impexus*, *Ste. pinicola* (≡ *Stp. amoena*), *Stp. hyperopta*, *Stp. microspora*, and *Ste. inconspicua*. If specimens are unavailable or lost, neotype designation becomes necessary; without this, future species descriptions may be impeded. Moreover, modern sequencing advances, especially by shallow sequencing of the genome, now enable valid sequence data from century-old specimens[88,158]. Therefore, future efforts should prioritize meticulous, comprehensive examinations of type specimens to resolve historical taxonomic issues and provide a solid voucher basis for systematic studies.

In summary, caution is warranted in delimiting taxa and inferring intrafamilial phylogenetic relationships, and further exploration for stable synapomorphies is needed. Future research should focus on: 1) Integrating type specimen localization with detailed morphological re-examination to strengthen taxonomic identification; 2) Applying molecular techniques, particularly shallow genome sequencing, to study critical type specimens and clarify the phylogenetic placement of problematic taxa; 3) Expanding sampling to cover broader geographical ranges, which is crucial for elucidating variation patterns within species complexes such as *Stp. hyperopta, Ste. fusca*, and *Sym. flaccidus*, revealing cryptic diversity, and clarifying species boundaries. Advancing these research avenues will significantly contribute to a more comprehensive understanding of the morphological evolution and phylogenetic structure within Stemonitidales.

Author contributions

The authors confirm contribution to the paper as follows: conceptualization: Song WL, Bortnikov FM, Novozhilov YK, Chen SL; data curation: Song WL, Bortnikov FM, Gmoshinskiy VI; funding acquisition: Chen SL, Novozhilov YK; investigation: Song WL, Bortnikov FM, Gmoshinskiy VI, Cai ML, Jiang ZQ; resources: Song WL, Bortnikov FM, Gmoshinskiy VI, Moroz EL, Vlasenko AV, Novozhilov YK, Chen SL; visualization: Song WL, Bortnikov FM, Gmoshinskiy VI; writing – original draft preparation: Song WL, Bortnikov FM, Gmoshinskiy VI, Novozhilov YK; writing – review and editing: Song WL, Bortnikov FM, Gmoshinskiy VI, Novozhilov YK, Chen SL. All authors reviewed the results and approved the final version of the manuscript.

Data availability

All data generated or analyzed during this study are included in this published article and its supplementary information files.

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Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

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References

[1] Adl SM, Bass D, Lane CE, Lukeš J, Schoch CL, et al. 2019. Revisions to the classification, nomenclature, and diversity of eukaryotes. *Journal of Eukaryotic Microbiology* 66:4–119

[2] Fiore-Donno AM, Nikolaev SI, Nelson M, Pawlowski J, Cavalier-Smith T, et al. 2010. Deep phylogeny and evolution of slime moulds (Mycetozoa). *Protist* 161:55–70

[3] Kang S, Tice AK, Spiegel FW, Silberman JD, Pánek T, et al. 2017. Between a pod and a hard test: The deep evolution of Amoebae. *Molecular Biology and Evolution* 34:2258–2270

[4] Leontyev DV, Schnittler M, Stephenson SL, Novozhilov YK, Shchepin ON. 2019. Towards a phylogenetic classification of the Myxomycetes. *Phytotaxa* 399:209–238

[5] Ruggiero MA, Gordon DP, Orrell TM, Bailly N, Bourgoin T, et al. 2015. A higher level classification of all living organisms. *PLoS ONE* 10:e0119248

[6] Lado C. 2005–2026. *An online nomenclatural information system of Eumycetozoa*. Madrid: Real Jardín Botánico, CSIC. https://eumycetozoa.com (Accessed on 16 Apr. 2026)

[7] Novozhilov YK, Rollins A, Shchepin ON, Schnittler M. 2022. Ecology and distribution of Myxomycetes. In *Myxomycetes (Second Edition)*, eds. Rojas C, Stephenson SL. New York: Academic Press. pp. 325–376 doi: 10.1016/B978-0-12-824281-0.00010-5

[8] Schnittler M, Dagamac NHA, Woyzichovski J, Novozhilov YK. 2022. Biogeographical patterns in Myxomycetes. In *Myxomycetes (Second Edition)*, eds. Rojas C, Stephenson SL. New York: Academic Press. pp. 377–416 doi: 10.1016/B978-0-12-824281-0.00009-9

[9] Hyde KD, Noorabadi MT, Thiyagaraja, He MQ, Johnston PR, et al. 2024. The 2024 Outline of Fungi and fungus-like taxa. *Mycosphere* 15:5146–6239

[10] Wijayawardene NN, Hyde KD, Al-Ani LKT, Tedersoo L, Haelewaters D, et al. 2020. Outline of Fungi and fungus-like taxa. *Mycosphere* 11:1060–1456

[11] Liu P, Zhang Z, Ge J, Zou Y, Li Z, et al. 2025. Dictyostelids: The second major group of slime molds. *Mycosphere* 16:423–516

[12] Keller HW, Everhart SE, Kilgore CM. 2022. The Myxomycetes: introduction, basic biology, life cycles, genetics, and reproduction. In *Myxomycetes (Second Edition)*, eds. Rojas C, Stephenson SL. New York: Academic Press. pp. 1–45 doi: 10.1016/B978-0-12-824281-0.00003-8

[13] Martin GW, Alexopoulos CJ. 1969. *The Myxomycetes*. Iowa: University of Iowa Press. 561 pp

[14] García-Martín JM, Zamora JC, Lado C. 2023. Multigene phylogeny of the order Physarales (Myxomycetes, Amoebozoa): shedding light on the dark-spored clade. *Persoonia* 51:89–124

[15] Prikhodko IS, Shchepin ON, Bortnikova NA, Novozhilov YK, Gmoshinskiy VI, et al. 2023. A three-gene phylogeny supports taxonomic rearrangements in the family Didymiaceae (Myxomycetes). *Mycological Progress* 22:11

[16] Ross IK. 1973. The Stemonitomycetidae, a new subclass of Myxomycetes. *Mycologia* 65:477–485

[17] Nannenga-Bremekamp NE, Lado C. 2022. *Descriptive, Illustrated Keys to the World's Myxomycetes*. Madrid: Consejo Superior de Investigaciones Científicas. 612 pp

[18] Poulain M, Meyer M, Bozonnet J. 2011. *Les myxomycètes*.Sevrier: Fédération mycologique et botanique Dauphiné-Savoie. 568+544 pp https://catalogue.bnf.fr/ark:/12148/cb42396890k

[19] Gmoshinskiy VI, Prikhodko IS, Bortnikov M, Shchepin ON, Novozhilov YK. 2023. New genus *Valtocarpus* (Myxomycetes = Eumycetozoa): molecular phylogeny and morphological analysis of aethalioid species in the order Stemonitidales. *Protistology* 17:216–232

[20] Fiore-Donno AM, Tice AK, Brown MW. 2019. A non-flagellated member of the Myxogastria and expansion of the Echinosteliida. *Journal of Eukaryotic Microbiology* 66:538–544

[21] Kretzschmar M, Kuhnt A, Bonkowski M, Fiore-Donno AM. 2016. Phylogeny of the highly divergent Echinosteliales (Amoebozoa). *Journal of Eukaryotic Microbiology* 63:453–459

[22] Ing B, Nannenga-Bremekamp NE. 1967. Notes on Myxomycetes XIII. *Symphytocarpus* nov. gen. Stemonitacearum. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and medical sciences* 70:218–231

[23] Nannenga-Bremekamp NE. 1974. *De Nederlandse Myxomyceten*. Zutphen: Bibliotheek van de Koninklijke Nederlandse Natuurhistorische Vereniging. 460 pp

[24] Nannenga-Bremekamp NE, Yamamoto Y, Sharma R. 1984. *Stemonaria*, a new genus in the Stemonitaceae and two new species of *Stemonitis* (Myxomycetes). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C, Biological and medical sciences* 87:449–469

[25] Fiore-Donno AM, Kamono A, Meyer M, Schnittler M, Fukui M, et al. 2012. 18S rDNA phylogeny of *Lamproderma* and allied genera (Stemonitales, Myxomycetes, Amoebozoa). *PLoS ONE* 7:e35359

[26] Eliasson UH, Sjögren L, Castillo A, Moreno G. 2010. Two species of the Stemonitales (Myxomycetes) new to Sweden. *Boletín de la Sociedad Micológica de Madrid* 34:43–50

[27] Strelow D, de Haan M, Bonkowski M, Fiore-Donno AM. 2020. New insights into the phylogeny of the dark-spored Myxomycetes (Amoebozoa : Conosa : Myxogastria : Fuscisporidia) and polyphyly of the genus *Stemonitis*. *Systematics and Biodiversity* 18:228–236
[28] Bortnikov FM, Bortnikova NA, Gmoshinskiy VI, Prikhodko IS, Novozhilov YK. 2023. Additions to *Trichia botrytis* complex (Myxomycetes): 9 new species. *Botanica Pacifica* 12:81–119
[29] Leontyev DV, Schnittler M, Stephenson SL. 2015. A critical revision of the *Tubifera ferruginosa* complex. *Mycologia* 107:959–985
[30] Lloyd SJ, Leontyev DV, Dagamac NHA. 2019. Three new species of *Tubifera* from Tasmania and New South Wales. *Phytotaxa* 414:240–252
[31] Leontyev DV, Schnittler M, Stephenson SL, Novozhilov YK. 2019. Systematic revision of the *Tubifera casparyi – T. dictyoderma* complex: resurrection of the genus *Siphoptychium* and introduction of the new genus *Thecotubifera*. *Mycologia* 111:981–997
[32] Leontyev D, Ishchenko Y, Schnittler M. 2023. Fifteen new species from the myxomycete genus *Lycogala*. *Mycologia* 115:524–560
[33] Leontyev D, Ishchenko Y, Leontieva M, Yatsiuk I, Shchepin O, et al. 2025. Expanding *Lycogala*: twenty-four new species, their morphology and phylogenetic relationships. *Fungal Systematics and Evolution* 16:93–146
[34] Song WL, Jiang ZQ, Li M, Leontyev D, Gao Y, et al. 2025. Comprehensive revision of *Lycogala* (Myxomycetes) in subtropical China: morphological and phylogenetic insights and ten new species. *IMA Fungus* 16:e147535
[35] Feng Y, Klahr A, Janik P, Ronikier A, Hoppe T, et al. 2016. What an intron may tell: several sexual biospecies coexist in *Meriderma* spp. (Myxomycetes). *Protist* 167:234–253
[36] Rammeloo J. 1975. Structure of the epispore in the Stemonitales (Myxomycetes) as seen with the scanning electron microscope. *Bulletin du Jardin Botanique National de Belgique / Bulletin Van de National Plantentuin Van België* 45:301–306
[37] Schnittler M, Leontyev D, Yatsiuk I, Ronikier A. 2025. Species descriptions in myxomycetes – can we settle on rules for good taxonomic practice? *IMA Fungus* 16:e141199
[38] Song WL, Chen SL. 2024. *Arcyria similaris*: A new myxomycete species from China. *Mycologia* 116:409–417
[39] Song WL, Li M, Wang ZQ, Chen SL. 2024. Taxonomy and phylogeny of three species in *Perichaena* sensu lato (Myxomycetes = Myxogastria) from China. *European Journal of Protistology* 95:e126105
[40] Fiore-Donno AM, Meyer M, Baldauf SL, Pawlowski J. 2008. Evolution of dark-spored Myxomycetes (slime-molds): Molecules versus morphology. *Molecular Phylogenetics and Evolution* 46:878–889
[41] Fiore-Donno AM, Novozhilov YK, Meyer M, Schnittler M. 2011. Genetic structure of two protist species (Myxogastria, Amoebozoa) suggests asexual reproduction in sexual Amoebae. *PLoS ONE* 6:e22872
[42] Novozhilov YK, Okun MV, Erastova DA, Shchepin ON, Zemlyanskaya IV, et al. 2013. Description, culture and phylogenetic position of a new xerotolerant species of *Physarum*. *Mycologia* 105:1535–1546
[43] Ronikier A, García-Cunchillos I, Janik P, Lado C. 2020. Nivicolous Trichiales from the austral Andes: unexpected diversity including two new species. *Mycologia* 112:753–780
[44] Wrigley de Basanta D, Estrada-Torres A, García-Cunchillos I, Cano Echevarría A, Lado C. 2017. *Didymium azorellae*, a new myxomycete from cushion plants of cold arid areas of South America. *Mycologia* 109:993–1002
[45] Lado C, Treviño-Zevallos I, García-Martín JM, Wrigley de Basanta D. 2022. *Diachea mitchellii*: A new myxomycete species from high elevation forests in the tropical Andes of Peru. *Mycologia* 114:798–811
[46] Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30:772–780
[47] Zamora JC, Rodrigues D, García-Cunchillos I, Lado C. 2025. First insights into the phylogeny of the order Cribrariales (Amoebozoa, Myxomycetes), with the definite exclusion of the genus *Enteridium*. *IMA Fungus* 16:e159960
[48] Xiang CY, Gao F, Jakovlić I, Lei HP, Hu Y, et al. 2023. Using PhyloSuite for molecular phylogeny and tree-based analyses. *iMeta* 20:348–355
[49] Zhang D, Gao F, Jakovlić I, Zou H, Zhang J, et al. 2020. PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. *Molecular Ecology Resources* 20:348–355
[50] Talavera G, Castresana J. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* 56:564–577
[51] Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermiin LS. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods* 14:587–589
[52] Minh BQ, Nguyen MAT, von Haeseler A. 2013. Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution* 30:1188–1195
[53] Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ. 2015. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32:268–274
[54] Lemoine F, Domelevo Entfellner JB, Wilkinson E, Correia D, Dávila Felipe M, et al. 2018. Renewing Felsenstein's phylogenetic bootstrap in the era of big data. *Nature* 556:452–456
[55] Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, et al. 2012. MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542
[56] Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematics and Evolution* 67:901–904
[57] Letunic I, Bork P. 2024. Interactive Tree of Life (iTOL) v6: recent updates to the phylogenetic tree display and annotation tool. *Nucleic Acids Research* 52:W78–W82
[58] Vlasenko A, Filippova N, Vlasenko V. 2020. A new epiphytic species, *Symphytocarpus macrosporus* (Myxomycetes) from Western Siberia, Russia. *Karstenia* 58:393–400
[59] Moreno G, Castillo A, Thüs H. 2018. Critical revision of type material of Stemonitales (Myxogastria) at the Natural History Museum London (BM). *Phytotaxa* 344:149–159
[60] Nannenga-Bremekamp NE, Härkönen M. 1979. *Symphytocarpus fusiformis* (Myxomycetes) a new species from Finland. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C* 82:371–374
[61] Kuhnt A. 2019. Bemerkenswerte Myxomycetenfunde: Neue Arten, Neukombinationen und Nachweise seltener Arten, Teil 2. *Berichte der Bayerischen Botanischen Gesellschaft zur Erforschung der Heimischen Flora* 89:139–222
[62] Zhang B, Wang S, Xu X, Li T, Dai D, et al. 2018. Identification of the new species *Comatricha macrospora* and two other recently recorded species of *Comatricha* from China. *Phytotaxa* 374:71–79
[63] Yamamoto Y. 1998. *The myxomycete biota of Japan*. Tokyo: Toyo Shorin Publishing Co. 700 pp
[64] Johannesen EW, Vetlesen P. 2020. New and rare myxomycetes (Mycetozoa, Myxogastria) in Norway, including a complete checklist of Norwegian myxomycete species. *AGARICA* 40:3–138
[65] Moreno G, Castillo A, Thüs H. 2024. Critical revision of Physarales and Reticulariales (Myxomycetes) at the Natural History Museum London (BM). *Phytotaxa* 644:79–101
[66] Moreno G., Illana C, Heykoop M. 1992. Spanish Myxomycetes. VI: Four interesting species belonging to the Stemonitales. *Cryptogamie Mycologie* 13:295–303
[67] Moreno G, Seraoui E-H, Meyer M, López-Villalba Á. 2023. A new species of *Macbrideola* on galls of Rosaceae. *Phytotaxa* 613:180–186
[68] Moreno G, Mitchell DW, Rojas C, Stephenson SL. 2010. A new species of *Stemonitis* (Myxomycetes) from Costa Rica. *Boletín de la Sociedad Micológica de Madrid* 34:231–236
[69] Vlasenko AV, Novozhilov YK, Prikhodko IS, Botyakov VN, Vlasenko VA. 2020. A new species of *Stemonitis pseudoflavogenita* from Russia, and the first record of *Stemonitis capillitionodosa* in Eurasia. *Phytotaxa* 447:137–145
[70] Novozhilov YK, Shchepin ON, Gmoshinskiy VI, Schnittler M. 2020. Myxomycetes of boreal forests of the Laplandskiy State Nature Biosphere Reserve (Kola Peninsula, Russia) Yuri. *Karstenia* 58(2):292–315

[71] Moreno G, Castillo A, Thüs H. 2020. Critical revision of *Stemonitis* and *Symphytocarpus* (Myxomycetes) at the Natural History Museum London (BM). *Phytotaxa* 458:257–280
[72] Neubert H, Nowotny W, Baumann K, Marx H. 2000. *Die Myxomyceten, Band 3 Stemonitales*. Gomaringen: Karlheinz Baumann Verlag. 391 pp
[73] Moreno G, Castillo A, Deschamps JR. 2013. Critical revision of myxomycetes in the buenos aires BAFC herbarium—1. *Mycotaxon* 123:63–79
[74] Yamamoto Y. 2021. *Biota of Japanese Myxomycetes*. Tsukubamirai: Committee for the publication of Biota of Japanese Myxomycetes. 1135 pp
[75] Moreno G, Castillo A, Deschamps JR. 2013. Critical revision of some Myxomycetes held at the Buenos Aires BAFC herbarium and the argentinian material kept in AH herbarium. III. *Boletín de la Sociedad Micológica de Madrid* 37:99–114
[76] Nannenga-Bremekamp NE. 1991. *A guide to temperate Myxomycetes, An English translation by A. Feest and Y. Burggraaf of de Nederlandse Myxomyceten*. Bristol: Biopress Ltd. 409 pp
[77] Moreno G, Singer H, Sánchez A, Illana C. 2004. A critical study of some Stemonitales of North American herbaria and comparison with European nivicolous collections. *Boletín de la Sociedad Micológica de Madrid* 28:21–41
[78] Moreno G, Rosing WC, Mitchell DW, Stephenson SL. 2007. *Comatricha pseudonigra*, a new corticolou myxomycete from Australia. *Boletín de la Sociedad Micológica de Madrid* 31:171–175
[79] Lister A. 1911. *A Monograph of the Mycetozoa, second edition*. London: The Trustees of the British Museum. 302 pp
[80] Peck CH. 1873. Descriptions of new species of fungi. *Bulletin of the Buffalo Society of Natural Sciences* 1:41–72
[81] Nannenga-Bremekamp NE, Yamamoto Y. 1988. *Stemonitis laxifila* (Myxomycetes), a new species from Nepal. *Crypt Himalayas* 1:29–30
[82] Doğan HH, Eroğlu G. 2014. A new *Stemonitis* species from Turkey. *Mycotaxon* 129:293–296
[83] Macbride TH. 1899. *The North-American Slime-moulds*. New York: The Macmillan Company. 231 pp
[84] Nannenga-Bremekamp NE, Yamamoto Y. 1990. Additions to the Myxomycetes of Japan IV. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C* 93:265–280
[85] Moreno G, Illana C, Burguete A. 1993. Spanish myxomycetes. *VII. (Province of Castellon). Mycotaxon* 46:407–424
[86] Moreno G, Lizárraga M, Esqueda M, Pérez-Silva E, Herrera T. 2006. Myxomycetes de Sonora, México. II: Reserva Forestal Nacional y Refugio de Fauna Silvestre Ajos-Bavispe. *Scientia Fungorum* 3:13–23
[87] Novozhilov YK, Mitchell DW. 2014. A new species of *Comatricha* (Myxomycetes) from southern Vietnam. *Novosti Sistematiki Nizshikh Rastenii* 48:188–195
[88] Shchepin ON, Prikhodko IS, Gmoshinskiy VI, Bortnikov FM, Dobriakova KD, et al. 2026. A multilocus phylogeny and updated system of the Columellomycetidae (Myxomycetes, Amoebozoa) based on low-pass genome sequencing data. *Fungal Diversity* In press
[89] Macbride TH. 1893. Nicaraguan myxomycetes. *Bulletin of the Laboratory of Natural History of iowa State University* 2:377–383
[90] Yamamoto Y. 1990. Two new species of Myxomycetes from Central Nepal. *Journal of Japanese Botany* 65:296–300
[91] Yamamoto Y, Nannenga-Bremekamp NE. 1995. Additions to the Myxomycetes of Japan V. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C* 98:317–326
[92] Rex GA. 1891. New American Myxomycetes. *Proceedings of the Academy of Natural Sciences of Philadelphia* 43:389–398
[93] Zhang B, Li Y. 2012. *Stemonaria liaoningensis*, sp. nov. (Myxomycetes, Stemonitidaceae) from northern China. *Sydowia* 64:329–333
[94] Ing B, Holland PC. 1967. New species of *Comatricha* and *Paradiachea*. *Transactions of the British Mycological Society* 50:685–686
[95] Lizárraga M, Moreno G, Esqueda M, Coronado ML. 2008. Myxomycetes of Sonora, Mexico. 4: Sierra de Alamos-Rio Cuchujaqui Biosphere Reserve. *Mycotaxon* 103:153–170
[96] Vlasenko AV, Moreno GH, Vlasenko VA. 2023. *Stemonitis amphorocolumella* (Stemonitidaceae, Myxomycetes), a new species from Western Siberia. *Phytotaxa* 592:59–67
[97] Lister A. 1894. *A monograph of the Mycetozoa*. London: The Trustees of the British Museum. 224 pp
[98] Bortnikov FM, Novozhilov YK, Stephenson SL. 2026. A comprehensive morphological study of type specimens of nine species of myxomycetes described from the United States in 1929–1986. *Phytotaxa* 742:255–277
[99] Nannenga-Bremekamp NE, Yamamoto Y. 1983. Additions to the Myxomycetes of Japan. I. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C* 86:207–241
[100] Castillo A, Moreno G, Illana C, Lago J. 1997. A critical study of some Stemonitales. *Mycological Research* 101:1329–1340
[101] Nannenga-Bremekamp NE. 1966. Notes on myxomycetes XI. Some new species of *Stemonitis*, *Comatricha*, *Badhamia*, *Physarum*, *Diderma* and *Didymium*. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C* 69:350–363
[102] Ing B. 1967. Notes on Myxomycetes. II. *Transactions of the British Mycological Society* 50:555–562
[103] Chen SL, Yan SZ, Li Y. 2010. An annotated checklist of Myxomycetes from Tibet, China. *Mycosystema* 29:845–851
[104] Wrigley de Basanta D, Stephenson SL, Lado C, Estrada-Torres A, Nieves-Rivera AM. 2008. Lianas as a microhabitat for myxomycetes in tropical forests. *Fungal Diversity* 28:109–125
[105] Yan SZ, Liu QS, Chen SL, Li Y. 2010. Notes on myxomycetes from Qinghai, China. *Mycosystema* 29:852–856
[106] Stephenson SL. 2021. *Secretive Slime Moulds. Myxomycetes of Australia*. Canberra, Melbourne: ABRS, CSIRO Publishing. 375 pp doi: 10.1071/9781486314140
[107] Lado C, Wrigley de Basanta D, Estrada-Torres A, Stephenson SL. 2016. Myxomycete diversity in the coastal desert of Peru with emphasis on the lomas formations. *Anales del Jardín Botánico de Madrid* 73:e032
[108] Peck ME, Gilbert HC. 1932. Myxomycetes of Northwestern Oregon. *The American Journal of Botany* 19:131–147
[109] Farr ML. 1988. Notes on Mycetozoa V. Corrections, redispositions and new taxa. *International journal of mycologie and lichenology* 3:199–213
[110] Massee G. 1892. *A Monograph of the Myxogastres*. London: Methuen & Co. 367 pp
[111] Lister A. 1925. *A monograph of Mycetozoa. 3rd edition*. London: Trustees of the British Museum. 296 pp
[112] Yamamoto Y. 2000. A new species of *Stemonitis* (Myxomycetes) from Japan. *Karstenia* 40:197–198
[113] Zhang B, Li Y. 2016. A new species, *Stemonitis sichuanensis*, and a newly recorded species, *Stemonitis marjana* (Myxogastria) from China. *Phytotaxa* 258:195–199
[114] Nannenga-Bremekamp NE, Yamamoto Y. 1987. Additions to the Myxomycetes of Japan. III. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C* 90:311–349
[115] Nannenga-Bremekamp NE. 1968. Notes on Myxomycetes XV. New species of *Oligonema*, *Licea*, *Clastoderma*, *Comatricha*, *Paradiacheopsis* and *Badhamia*. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C* 71:41–51
[116] Novozhilov YK. 1986. Myxomycetes of the USSR. III. Genus *Macbrideola* H. C. Gilbert. *Mycology and phytopathology* 20:102–105 (in Russian with Latin diagnoses)
[117] Ejale A. 2010. *Myxomycetes from Southern Nigeria*. Saarbrücken, Germany: LAP LAMBERT Academic Publishing. 426 pp
[118] Meylan C. 1918. Myxomycètes nouveaux. *Bulletin de la Société Vaudoise des Sciences Naturelles* 52:95–97 (in French)
[119] Castillo A, Moreno G, Illana C. 1993. A new species of *Comatricha* with incompletely reticulated spores from Spain. *Mycotaxon* 46:315–319
[120] Sakulin SV, Gmoshinskiy VI, Kireeva NI. 2025. First record of *Comatricha meandrispora* (Myxomycetes) in Russia. *Mycology and phytopathology* 59:548–552
[121] Bratteng AS. 1975. *Comatricha orthotricha*, a new species of Myxomycete. *Mycologia* 67:413–417
[122] Farr ML. 1987. A new species of *Comatricha* from Colorado. *Mycotaxon* 30:455–458
[123] Salamaga A, Grzesiak B, Kochanowska M, Kochanowski J. 2014. *Symphytocarpus trechisporus* (Myxogastrea) in Poland. *Polish Botanical Journal* 59:279–283

[124] Ehrenberg CG. 1818. *Sylvae mycologicae berolinense* (in Latin). Berolini (Berlin): Formis Theophili Bruschcke. 32 pp. https://catalog.hathitrust.org/Record/011693278
[125] Farr ML. 1976. *Flora Neotropica. Monograph No. 16. Myxomycetes*. New York: The New York Botanical Garden. 304 pp
[126] Lado C, Wrigley de Basanta D, Estrada-Torres A, Stephenson SL, Treviño I. 2019. Diversity of Myxomycetes in arid zones of Peru part II: the cactus belt and transition zones. *Anales del Jardín Botánico de Madrid* 76:e083
[127] Macbride TH, Martin GW. 1934. *The Myxomycetes: A Descriptive List of the Known Species with Special Reference to Those Occurring in North America*. New York: The Macmillan Company. 339 pp
[128] Martin GW. 1949. *Fungi. Myxomycetes. Ceratiomyxales, Liceales, Trichiales, Stemonitales, Physarales*. New York: The New York Botanical Garden. 190 pp
[129] Lado C, Wrigley de Basanta D. 2018. Typification of the myxomycete taxa described by the Listers and preserved at the Natural History Museum, London (BM). *Phytotaxa* 341:1–83
[130] Zhang B, Li Y. 2017. A new *Stemonitis* species and a new record of *Elaeomyxa* from China. *Phytotaxa* 323:83–87
[131] Vlasenko AV, Filippova NV, Vlasenko VA. 2022. First Russian records of *Stemonitis rhizoideipes* and *Fuligo aurea*, and newly observed morphology for *Comatricha anomala*. *Mycotaxon* 137:371–380
[132] Rostafinsky J. 1874. *Śluzowce (Mycetozoa) Monografia* (in Polish). Paris: Towarzystwo Nauk Ścisłych w Paryżu. 215 pp
[133] Jaczewski AA. 1907. *Mycological flora of European and Asian Russia. Volume II. Slime moulds* (in Russian). Moscow: V. Richter's Typo-lithography. 410 pp
[134] Nannenga-Bremekamp NE. 1973. Notes on Myxomycetes XIX. *Proceedings van de Koninklijke Nederlandse Akademie van Wetenschappen Section C* 76:476–488
[135] Moroz EL, Gmoshinskiy VI, Shchepin ON, Novozhilov YK. 2024. The Systematics and phylogeny of Myxomycetes: yesterday, today, and tomorrow. *Doklady Biological Sciences* 519:356–369
[136] Song CG, Xu TM, Xu YH, Wang D, Zeng L, et al. 2025. Systematic revision, molecular phylogeny and divergence times of Thelephorales (Basidiomycota). *Mycosphere* 16:296–422
[137] Treviño-Zevallos I, García-Cunchillos I, Wrigley de Basanta D, Lado C. 2023. Diversity of Myxomycetes from Peru Part III: the high Andes and the altiplano. *Phytotaxa* 624:1–92
[138] Wrigley De Basanta D, Lado C, Estrada-Torres A, Stephenson SL. 2013. Biodiversity studies of myxomycetes in Madagascar. *Fungal Diversity* 59:55–83
[139] Shchepin O, Novozhilov Y, Woyzichovski J, Bog M, Prikhodko I, et al. 2022. Genetic structure of the protist *Physarum albescens* (Amoebozoa) revealed by multiple markers and genotyping by sequencing. *Molecular Ecology* 31:372–390
[140] Shchepin ON, López Villalba Á, Inoue M, Prikhodko IS, Erastova DA, et al. 2024. DNA barcodes reliably differentiate between nivicolous species of *Diderma* (Myxomycetes, Amoebozoa) and reveal regional differences within Eurasia. *Protist* 175:e126023
[141] Leontyev D, Buttgereit M, Kochergina A, Shchepin O, Schnittler M. 2023. Two independent genetic markers support separation of the myxomycete *Lycogala epidendrum* into numerous biological species. *Mycologia* 115:32–43
[142] Gøtzsche HF, Woerly B, Popa F, Shchepin ON, Prikhodko IS, et al. 2025. A new species of *Diacheopsis* (Myxomycetes) and a new habitat for myxomycetes. *Mycologia* 117:183–200
[143] Fiore-Donno AM, Clissmann F, Meyer M, Schnittler M, Cavalier-Smith T. 2013. Two-gene phylogeny of bright-spored Myxomycetes (slime moulds, superorder Lucisporidia). *PLoS ONE* 8:e62586
[144] García-Cunchillos I, Estébanez B, Lado C. 2021. Spore ultrastructural features and significance of their diverse ornamental elements in the evolutionary history of the order Trichiales (Myxomycetes, Amoebozoa). *European Journal of Protistology* 81:e125839
[145] García-Cunchillos I, Zamora JC, Ryberg M, Lado C. 2022. Phylogeny and evolution of morphological structures in a highly diverse lineage of fruiting-body-forming amoebae, order Trichiales (Myxomycetes, Amoebozoa). *Molecular Phylogenetics and Evolution* 177:e107609
[146] Zhang B, Li Y. 2016. A new species and two new records of Stemonitidaceae from China. *Phytotaxa* 267:151–156
[147] Moreno G, Sánchez A, Castillo A. 2023. *Paradiacheopsis rigida* (Myxomycetes): a misinterpreted species. *Boletín de la Sociedad Micológica de Madrid* 47:3–8
[148] Woyzichovski J, Shchepin ON, Schnittler M. 2022. High environmentally induced plasticity in spore size and numbers of nuclei per spore in *Physarum albescens* (Myxomycetes). *Protist* 173:e125904
[149] Leontyev DV. 2016. The evolution of sporophore in Reticulariaceae (Myxomycetes). *Ukrainian Botanical Journal* 73:178–184
[150] Zamora JC, García-Martín JM, Lado C. 2023. (2955) Proposal to conserve the name *Didymium* against *Mucilago* and *Spumaria* (Physarales, Myxomycetes). *Taxon* 72:663–664
[151] Zhao FY, Liu SY, Stephenson SL, Hsiang T, Qi B, et al. 2021. Morphological and molecular characterization of the new aethaloid species *Didymium yulii*. *Mycologia* 113:926–937
[152] Ronikier A, Janik P, de Haan M, Kuhnt A, Zankowicz M. 2022. Importance of type specimen study for understanding genus boundaries—taxonomic clarifications in *Lepidoderma* based on integrative taxonomy approach leading to resurrection of the old genus *Polyschismium*. *Mycologia* 114:1008–1031
[153] Keller HW, Aldrich HC, Brooks TE, Schoknecht JD. 1975. The taxonomic status of *Badhamia ovispora*: a myxomycete with unique spores. *Mycologia* 67:1001–1011
[154] Gmoshinskiy VI, Peters DA, Kireeva NI, Perevedentseva LG. 2025. First records of *Badhamia ovispora* (Physarales, Myxomycetes) in Russia. *Novosti sistematiki nizshikh rastenii* 59:F1–F9
[155] Gmoshinskiy VI, Bortnikov FM. 2025. Critical revision of the myxomycete (Myxomycota, Myxomycetes) collection at the A.A. Jaczewski mycological herbarium (LEP): II. Type collection. *Natural History Collections and Museomics* 2:1–18
[156] Gmoshinskiy VI, Kireeva NI, Sakulin SV, Matveev AV, Novozhilov YK. 2025. Critical revision of the myxomycete (Myxomycetes, Myxomycota) collection at the Mycological herbarium LEP. I. Yaroslavl Region. *Turczaninowia* 28:36–50
[157] Wrigley de Basanta D, Mier CD, Lado C. 2023. A taxonomic revision of species in the subgenus *Licea* (*Licea* subg. *Licea*, Myxomycetes). *Phytotaxa* 629:95–128
[158] Nevill PG, Zhong X, Tonti-Filippini J, Byrne M, Hislop M, et al. 2020. Large scale genome skimming from herbarium material for accurate plant identification and phylogenomics. *Plant Methods* 16:1

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