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Gymnopilus penetrans and *G. swaticus sp. nov*. (Agaricomycota: Hymenogastraceae); a new record and a new species from northwest Pakistan

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Abstract

Two *Gymnopilus* species are described and illustrated from northern parts of Khyber Pakhtunkhwa province, Pakistan. *Gymnopilus swaticus* is described as new to science based on morphological characters and data from nITS and nLSU. *Gymnopilus penetrans* is a new record for Pakistani mycobiota.

Keywords: agaricoid fungi, DNA sequences, molecular phylogeny, Swat district, taxonomy

Introduction

Gymnopilus P. Karst. (1879: 400) is an agaricoid genus in the family *Hymenogastraceae* (Kirk *et al.* 2008), that mostly includes wood-inhabiting fungi (Holec 2005). Molecular approaches have supported its monophyly (e.g., Guzmán-Dávalos *et al.* 2003). It is represented by more than 200 different species of worldwide distribution (Kaur *et al.* 2015). Members of the genus are characterized by yellow, ferruginous, or purple fruiting bodies, a saprotrophic nature, the presence of cortinoid to membranous veil, and a rusty brown spore print (Kaur *et al.* 2015). Microscopically, the identity to the genus is confirmed by roughened basidiospores that range from verrucose to rugulose, capitate to subcapitate ventricose cheilocystidia, and clamp connections present on almost all kinds of hyphae (Kühner 1980; Singer 1986). The shape and size of the spores and cystidia are considered important characters for distinction among the species (Rees *et al.* 2004). Additionally, the position of other types of cystidia, the arrangement of cells in the sub-hymenium, and the orientation of hyphae of the pileal trama are also relevant (Guzmán-Dávalos *et al.* 2003). The genus was classified into several infrageneric groups based on the type of velar remains (Singer 1951; Hesler 1969; Guzmán-Dávalos 1995; Rees *et al.* 2002).

The genus has been little explored in Pakistan and only six species are previously reported (Ahmad *et al.* 1997). These include; *G. aeruginosus* (Peck) Singer (1951: 560), *G. chrysimyces* (Berk.) Manjula (1983: 90), *G. chrysites* (Berk.) Singer (1962: 76), *G. hybridus* (Gillet) Maire (1933: 96), *G. junonius* (Fr.) P.D. Orton (1960: 176), and *G. sapineus* (Fr.) Murrill (1912: 254). In this paper, two species of *Gymnopilus* are being presented, *G. swaticus*, a new species, and *G. penetrans* (Fr.) Murrill (1912: 254), a new record from Pakistan.

Material and methods

Field work and study of macro-characters

Collections were made on routine mycological field visits to moist temperate forests of Miandam and Lalkoo valleys of the Swat district, in northern areas of Khyber Pakhtunkhwa province, Pakistan. Basidiomes were collected with care using a sharp knife and field notes were made regarding habitat, substrate, and surrounding vegetation. Macro-morphological characters were observed from fresh specimens considering all the available basidiomes. Color codes followed Munsell (1975) and were annotated in parenthesis after common color names. Properly dried and preserved

specimens were deposited in the Swat University Herbarium (SWAT) and in the Herbarium of the University of the Punjab (LAH), both in Pakistan.

Study of micro-characters

A light microscope (BM 120, Boeco, Germany) fitted with a microscopic camera (MVV, 3000) was used for microscopic analyses. Tissues were rehydrated using distilled water and mounts were prepared in 5% potassium hydroxide (KOH) solution and stained with 1% Congo Red for contrast following Rees *et al.* (2002). Melzer's reagent was used for checking the amyloidy of basidiospores. For measurements, a calibrated computer based software (Piximetre) was used. The readings in parenthesis represent extreme values, Me is the mean of spore measurements, Q represents the length / breadth ratio of individual spores, and Qe represent average length / breadth ratio of all the spores from all basidiomes. For a thorough observation, slides were prepared from all the available basidiomes. For basidiospore measurements, 20 randomly selected spores were measured from each basidiome. Basidial measurements were without sterigmata while basidiospore measurements were without apiculus and ornamentation (Rees *et al.* 2002).

Molecular work

DNA extraction and polymerase chain reaction (PCR) amplifications

DNA was extracted from a small piece (5–10 mg) of lamellae of dried specimens using the CTAB method of Gardes & Bruns (1993). The universal primer pair ITS1F (forward) (Gardes & Bruns, 1993) and ITS4 (reverse) (White *et al.* 1990) was used to amplify the ITS (ITS1-5.8S-ITS2) rDNA region. PCR procedure for ITS region consisted of initial 4 min denaturation at 94°C, 40 cycles of 1 min at 94°C, 1 min at 55°C, 1 min at 72°C, and a final extension of 10 min at 72°C. The primer pair LR5 and LR0R (Vilgaly's lab http://sites.biology.duke.edu/fungi/mycolab/primers.htm) was used to amplify the rDNA large sub unit (LSU). PCR procedure for LSU region consisted of initial denaturation at 94°C for 2 min, then 35 cycles of 94°C for 1 min, 52°C for 1 min, 72°C for 1 min, and final extension at 72°C for 7 min. Visualization of PCR products was accomplished using 1% agarose gel with 3 µl ethidium bromide added and a UV illuminator. Sequencing of the amplified products was done in the Beijing Genomic Institute, Hong Kong.

Phylogenetic studies

For phylogenetic analysis, the ITS and LSU sequences generated from the Pakistani collections were compared with other sequences in GenBank using Basic Local Alignment Search Tool (BLAST) (Altschul *et al.* 1990). Based on the outcome, closely matched sequences and those mentioned in Moser *et al.* (2001) and Guzmán-Dávalos *et al.* (2003) were downloaded for phylogenetic analysis. Two separate matrices were created for ITS and LSU. Sequences were aligned using online webPRANK tool at http://www.ebi.ac.uk/goldman-srv/webprank/ (Löytynoja & Goldman 2010). Maximum Likelihood (ML) analyses were performed for individual gene regions using CIPRES Science Gateway (Miller *et al.* 2010) and employing RAxML-HPC v.8. rapid bootstrap analysis/search for best-scoring ML tree. For the bootstrapping phase, the GTRGAMMA model was selected and one thousand rapid bootstrap replicates were run.

Results

Molecular phylogenetic analyses (Figures 1 & 2)

The ITS matrix contained 63 sequences with *Hebeloma fastibile* (Pers.) P. Kumm. (1871:80) (AF325643) and *H. pusillum* J.E. Lange (1938: 6) (KF309422) as outgroup taxa. There was a total of 653 positions in the aligned dataset. The ITS based cladogram (Figure 1) of *Gymnopilus* species is represented by eight clades in which the position of the taxa was according to previous studies (Rees *et al.* 2002; Guzmán-Dávalos *et al.* 2003; 2008; 2009).

In the LSU dataset, 30 sequences were used with *Hebeloma fastibile* (AY033139) and *H. pusillum* (JN939968) as the outgroup taxa. There was a total of 812 characters in the aligned dataset. Due to low number of available sequences in the GenBank, LSU based phylogeny did not correspond to that of ITS; however, it confirmed the unique position of *Gymnopilus swaticus* (Figure 2).

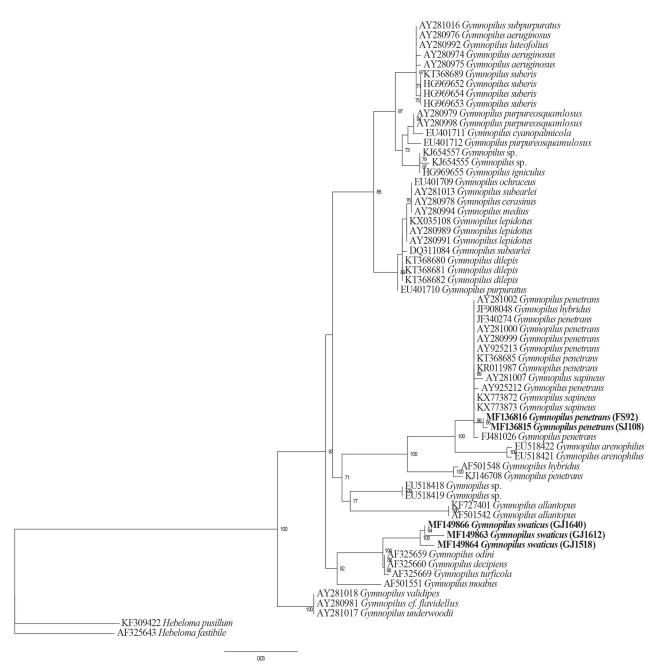


FIGURE 1. Phylogenetic tree with the highest likelihood of the ITS rDNA dataset from *Gymnopilus* inferred by Maximum Likelihood. The sequences generated during this study are represented in bold. Bootstrap values \geq 70% are shown.

Taxonomy

Gymnopilus penetrans (Fr.) Murrill (1912: 254) (Figures 3E–F, 4)

Description:—*Pileus* 40–55 mm across, convex to plano-convex when young, becoming hemispherical to plano-convex to slightly concave at maturity, with inflexed to involute margin, yellow ochre to rusty brown (2.5YR7/8-2.5YR6/8), smooth or slightly wrinkled in dried specimens, glabrous, context pale yellow (2.5Y8/8), thicker at the center. *Lamellae* emarginate with a small decurrent tooth, crowded to close, rusty yellow (5YR6/6) to deep rusty brown (5YR5/6), at places stained with dark rusty brown spots, edge concolorous or somewhat paler, irregularly serrulate. *Stipe* 70–95 × 5–8 mm, central to slightly eccentric, cylindrical or gradually thickening downward, pale ochre (5YR8/2), brownish to rusty brown (5YR8/6), with or without white fibrillose partial veil remnants, base with white mycelium.

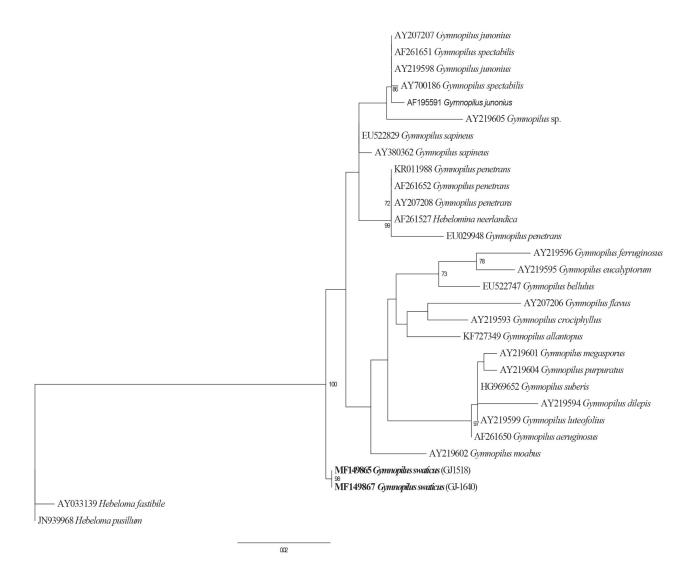


FIGURE 2. Phylogenetic tree with the highest likelihood of the LSU dataset from *Gymnopilus*. The sequences generated during this study are represented in bold. Bootstrap values \geq 70% are shown.

Basidiospores (6.6–) 7.2–9.9 (–10.6) × (3.7–) 4–5.5 (–6.1) µm, Me = 8.7 × 5 µm, Q = 1.6–1.9, Qe = 1.8, ellipsoid to oblong, vertucose to rugulose-vertucose, ornamentation moderately developed, not more than 0.2 µm high, mature spores distinctly red-brown in Melzer's reagent (dextrinoid), yellowish brown in KOH. *Basidia* 20–27 × 5.8–7.4 µm, 4-spored, average sterigmata length 4.6 µm, narrowly clavate to more or less narrowly utriform. *Cheilocystidia* 20–30 × 6–8 µm, cylindrical, narrowly utriform to lecythiform, capitate to sub-capitate, hyaline. *Pleurocystidia* 15–20 × 6–8 µm, narrowly lageniform with globose head or utriform, hyaline. *Pileipellis* a cutis, hyphae 3–6 µm in diameter, interwoven, rusty brown, clamped septa frequent, no pileocystidia observed. *Stipitipellis* with hyphae 4–6 µm in diameter, more or less parallel, hyaline, clamped at septa.

Materials examined:–PAKISTAN. Khyber Pakhtunkhwa province, Dir Upper district, Kumrat valley, 2500 m a.s.l., solitary, on mulch rich soil under *Pinus wallichiana*, 2 September 2015, *A.N. Khalid FS92* (LAH35271!); Swat district, Miandam, 2250 m a.s.l., in small group, on mulch-rich soil under *Picea smithiana*, 5 September 2013, *Sana Jabeen SJ108* (LAH35131!).

Gymnopilus swaticus J. Khan, Sher & Khalid sp. nov. (Figures 3A-D, 5)

MycoBank number:-MB820555

Etymology:---the specific epithet "swaticus" refers to the district of collection, Swat.

Diagnosis:—growth on *Piceae smithiana*, fruiting body 40–70 mm across, pileus velutinous to slightly tomentose, subdistant to close and sinuate to emarginate lamellae, ellipsoid to amygdaliform basidiospores measuring $8.6-10.0 \times 4.5-5.6 \mu m$.

Type:—PAKISTAN. Khyber Pakhtunkhwa province, Swat district, Gabin Jabba valley Lalkoo, in decomposing cavities of *Picea smithiana*, 2483 m a.s.l., 31 August 2015, *Junaid Khan GJ-1518* (Holotype SWAT000133!).

GYMNOPILUS PENETRANS AND G. SWATICUS SP. NOV.

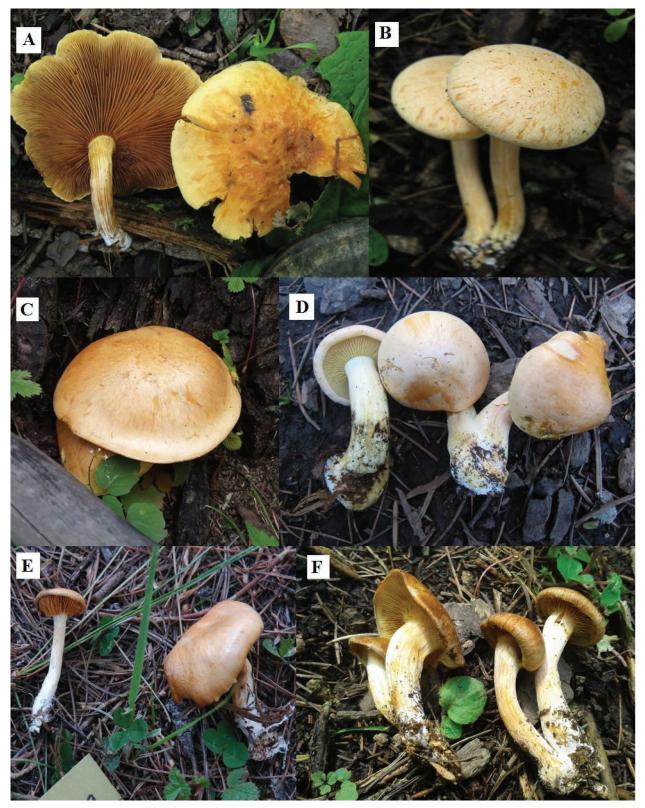


FIGURE 3. Basidiomes in natural habitat. A–D. *Gymnopilus swaticus*, A–B. Holotype collection, C. SWAT000134, D. LAH35300. E–F. *Gymopilus penetrans*, E. LAH35271, F. LAH35131. Photos by Junaid Khan.

Description:—*Pileus* 40–70 mm across, hemispherical, convex or campanulate when young, plano-convex to plane at maturity, margin incurved to inrolled at first, becoming straight with age, yellowish orange (2.5YR8/4) to light orange (2.5YR4/6) when young, rusty yellowish orange (2.5YR5/12 to 2.5YR6/12) by maturity, surface dry, dull, pruinose to velutinous when young, velutinous to pubescent or slightly tomentose later on, context moist, solid, thicker at the center (≤ 9 mm), flesh concolorous with pileus or paler, continuous with the stipe, compact, unchanging upon cutting.

Lamellae sinuate to emarginate, broad (≤ 7 mm), sub-distant to close, sulphur yellow (2.5YR5/12 to 2.5YR6/12) when young, turning rusty brown (2.5YR5/12 to 2.5YR6/12) with age with a paler margin, edge entire or slightly serrulate, lamellulae mostly in 3 tiers. *Stipe* 40–70 × 8–12 mm, central to slightly eccentric, terete, equal, concolorous with the pileus (2.5YR8/4 to 2.5YR4/6), velutinous to fibrillose, longitudinally striate, base covered with white mycelium especially in young stages, texture firm, interior solid, flesh concolorous with the stipe or slightly darker, especially at the center.

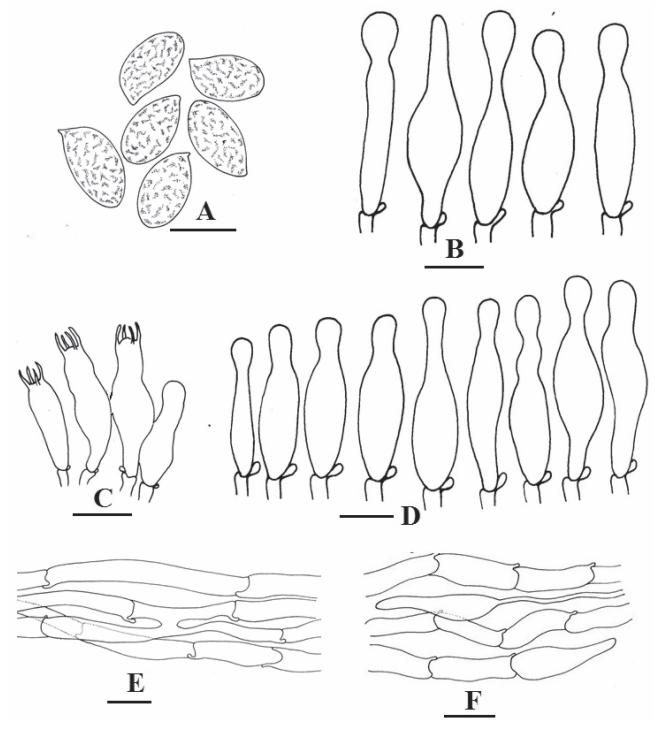


FIGURE 4. Microscopic structures of *Gymnopilus penetrans* (LAH35271). A. Basidiospores. B. Cheilocystidia. C. Basidia. D. Pleurocystidia. E. Stipitipellis. F. Pileipellis. Scale bar = $10 \mu m$ for A–B; $8 \mu m$ for C–D; $6 \mu m$ for E–F. Drawings by Munazza Kiran.

Basidiospores (8–) 8.6–10 (–10.5) × (3.9–) 4.5–5.6 (–6) μ m, Me = 9.1 × 5.1 μ m, Q = (1.6–) 1.7–2.1 (–2.3), Qe = 1.8, mostly ellipsoid to elongate, amygdaliform, rarely ovoid, vertucose, ornamentation 0.3–0.5 μ m high, plage and germ pore absent, dextrinoid in Melzer's reagent, dark brown in KOH. *Basidia* 30–35 × 6–8 μ m, narrowly clavate,

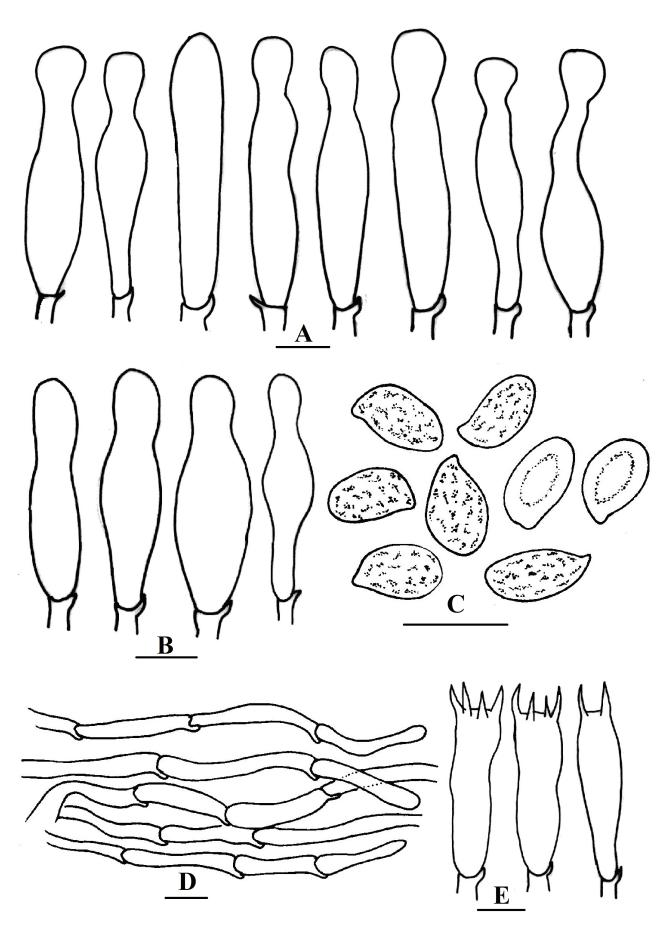


FIGURE 5. Microscopic characters of *Gymnopilus swaticus* (SWAT000133). A. Cheilocystidia. B. Pleurocystidia. C. Basidiospores. D. Pileipellis. F. Basidia. Scale bar = 10 μm for A & C; 8 μm for B, D & E. Drawings by Junaid Khan.

mostly 4-sterigmate, rarely 2-sterigmate, sterigmata $\leq 5 \mu m$ long, clamped at the bases, hyaline. *Cheilocystidia* 35–40 \times 8–10 μm , scattered, narrowly utriform, narrowly lageniform, cylindrical, narrowly clavate, with capitate to subcapitate heads, hyaline to slightly golden brown. *Pleurocystidia* 30–35 \times 6–8 μm , narrowly utriform, slightly projecting. *Pileipellis* a cutis, hyphae 4–6 μm in diameter, clamped, hyaline to slightly brown, with cylindrical terminal elements. *Subhymenium* ramose-inflated, hyphae $\leq 20 \mu m$ in diameter, with clamps, hyaline.

Habitat:—in small scattered groups, in decomposing cavities of standing trees of Picea smithiana.

Additional specimens examined:—PAKISTAN. Khyber Pakhtunkhwa province, Swat district, Gabin Jabba valley Lalkoo, 2483 m a.s.l., 8 July 2016, *Junaid Khan GJ-1640* (SWAT000134!); 15 September 2016, *Junaid Khan GJ-1612* (LAH35300!).

Known distribution:-Pakistan, Khyber Pakhtunkhwa province, Swat district, Gabin Jabba valley.

Discussion

This study reports two species of *Gymnopilus*, i.e., *G. penetrans* and *G. swaticus sp. nov.* from Khyber Pakhtunkhwa province, Pakistan. Phylogenetically, the two *G. penetrans* collections (FS92 and SJ108) clustered with other ITS sequences of *G. penetrans* or sequences of this complex, as *G. hybridus* (Gillet) Maire and *G. sapineus* (Fr.) Murrill (Figure 1). It is a common but very variable species, characterized by medium-sized basidiomes, a smooth pileus (Clémençon 2002), the presence of a partial veil in young specimens, and moderately ornamented medium-sized basidiospores (Holec 2005). The species is normally lignicolous, growing on conifer logs (Holec 2005). This species is widespread in distribution and is reported from varied ecological regions including Britain, Ireland, Europe (from Scandinavia down to the Mediterranean region), North Africa, and many parts of North America (Davis *et al.* 2012). In this study, it is being presented as the first record from Pakistan.

Gymnopilus swaticus is a newly described taxon, that clustered along with G. decipiens (W.G. Smith) P.D. Orton (1960: 176), G. fulgens (J. Favre et Maire) Singer (1951: 561), G. odini (Fr.) Bon & P. Roux. (2002: 10), and G. turficola M.M. Moser & H. Ladurner in Moser et al. (2001: 323) (Figure 1). A comparison with these taxa is presented in Table 1. Morphologically, G. swaticus shares with G. decipiens a somewhat similar tomentose-fibrillose pileal surface, a finely floccose to fibrillose scaly stipe, basidiospores of almost the same size, and the presence of cheilocystidia and pleurocystidia (Høiland 1990; Orton 1993; Holec 2005). However, G. decipiens differs from G. swaticus mainly in its habitat, on soil especially sandy and burnt soil of conifer dominated forests (including *Picea*), has a smaller fruiting body (\leq 30 mm), cheilocystidia of variable shape (narrowly lageniform-fusiform, broadly lageniform, utriform, fusiform-cylindrical), and rare, narrowly utriform pleurocystida (Høiland 1990; Orton 1993). Gymnopilus turficola also resembles G. swaticus in its involute margin, tomentose-fibrillose pileal surface, color of the young and mature pilei, fibrillose stipe without an annulus, presence of cheilocystidia and pleurocystidia, and basidiospores of almost same size and shape. Yet, this species can also be differentiated by its habitat in palsa mires growing on peat in subarctic areas, greenish lamellae in young stages, the development of an iodoform odor when kept closed for some hours, bottle-shaped cheilocystidia and pleurocystidia, and the presence of caulocystidia (Moser et al. 2001). Gymnopilus odini is another species falling within the same clade, differing from G. swaticus by its habitat on sandy to peaty soil, more vividly colored pileus (orange red-brown), almost smooth pileal surface (at most finely fibrillose-scaly), and shorter basidiospores measuring $6.5-7.5 \times 4.0-4.8 \ \mu m$ (Høiland 1990; Orton 1993; Ludwig 2001). Gymnopilus fulgens can be distinguished by its smaller fruiting body, orange-yellow to reddish brown pileal color, stipe with red-brown lower part, somewhat larger and broader basidiospores (8–11 \times 5–7 μ m), and absence of pleurocystidia (Holec 2005).

It also seems reasonable to compare the present Pakistani collections with some other Asian taxa. *Gymnopilus junonius* (Fr.) P.D. Orton reported from Pakistan, can be separated by its habitat (mainly on *Quercus* species), stipe with ring, and capitate to sub-capitate ventricose cystidia (Rees & Strid 2001). *Gymnopilus bryophilus* Murrill (1913: 22) reported from India, resembles *G. swaticus* in its velutinous to finely floccose orangish fruiting bodies, incurved margin, eccentric stipe in older specimens, sub-distant to close sinuate lamellae, fibrillose stipe, whitish mycelium at the base and narrowly utriform cheilocystidia with subcapitate heads (Thomas *et al.* 2003). However, the former is distinguished by smaller basidiospores ($5.2-7.2 \times 4.2-4.8 \mu m$) and absence of pleurocystidia. *Gymnopilus terricola* K.A. Thomas, Guzm.-Dáv. & Manim. (2003: 302) is similar in having a tomentose pileus and sinuate lamellae. However, this species differs from *G. swaticus* in its habitat on soil, smaller fruiting body, hollow stipe with a bluish grey lower part, smaller basidiospores ($6.5-8.4 \times 5.2-6 \mu m$), and absence of pleurocystidia (Thomas *et al.* 2003).

Characters/species	G. swaticus	G. turficola	G. decipiens	G. odini	G. fulgens
Habitat	On Picea smithiana	Peat in palsa mires	Sandy to peaty soil or burnt ash/ charcoal in <i>Picea</i> or <i>Pinus</i> forests	Sandy to peaty soil or burnt areas in coniferous forests	Peat or peaty soil among <i>Sphagnum</i> and other mosses
Pileus/stipe diameter (mm)	40-70/8-12	8-40/2-7	7–27/2–4	15-25/1.5-2.5	12-22/1.5-2.5
Pileus ornamentation	Velutinous to slightly tomentose	Tomentose-fibrillose to appressed scaly	Fibrillose-felty or scaly with felty squamules	Smooth and glabrous, at most finely fibrillose scaly	Smooth and glabrous
Veil	Absent	Absent	With weak veil remnants	Absent	Absent
Basidiospores (Size μm)	8.6–10.0 × 4.5–5.6	7.1–10 × 4.1–5.3	7.2–9.2 × 4.0–5.2	6.5–7.5 × 4.0–4.8	8–11 × 5–7
Q (l/w ratio)	1.7–2.1 Ellipsoid to	1.5–2.0 Ellipsoid to	1.6–1.8 Amygdaliform	1.5–1.7 Ovoid-ellipsoid to	1.5–1.7 Amygdaliform to
Shape	amygdaliform	subamygdaliform	to narrowly amygdaliform	amygdaliform	ellipsoid
Suprahilar depression	Absent	Absent	Absent	Absent	Present
Cheilocystidia (µm)	$35 - 40 \times 8 - 10$	$30 - 38 \times 6 - 8$	$20 - 32 \times 6 - 8$	No data	$24 - 28 \times 5 - 7$

TABLE 1. Comparison of important characters of Gymnopilus swaticus and related species.

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References

Ahmad, S., Iqbal, S. & Khalid, A.N. (1997) Fungi of Pakistan. Sultan Ahmad Mycological Society of Pakistan, Lahore, pp. 1–248.

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman, D.J. (1990) Basic local alignment search tool. *Journal of Molecular Biology* 215: 403–410.

https://doi.org/10.1016/S0022-2836(05)80360-2

Bon, M. & Roux, P. (2002) Le genre Gymnopilus Karst. en Europe. Fungi non Delineati 17: 1-52.

Clémençon, H. (2002) Mycelial morphology, rhizomorph anatomy and primordium formation of *Gymnopilus penetrans*. *Feddes Repertorium* 113: 63–79.

https://doi.org/10.1002/1522-239X(200205)113:1/2<63::AID-FEDR63>3.0.CO;2-Q

- Davis, M., Sommer, R. & Menge, J. (2012) *Field guide to mushrooms of western North America (Vol. 106)*. University of California Press, Berkeley, California, pp. 246–247.
- Gardes, M. & Bruns, T.D. (1993) ITS primers with enhanced specificity for basidiomycetes-application to the identification of mycorrhizae and rusts. *Molecular Ecology* 2: 113–118.

https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Guzmán-Dávalos, L. (1995) Further investigations on *Gymnopilus* (Agaricales, Cortinariaceae). A new section and a new species from Mexico. *Mycotaxon* 54: 117–124.

Guzmán-Dávalos, L. (2003) Type studies of Gymnopilus (Agaricales) I. Mycotaxon 86: 395-423.

Guzmán-Dávalos, L., Contu, M., Ortega, A., Vizzini, A., Herrera, M., Ovrebo, C., Rodríguez, A., Villalobos-Arámbula, A.R., Palomera, V., Vargas, G. & Santerre, A. (2008) New morphological and molecular data on *Gymnopilus purpureosquamulosus* and its phylogenetic relationships among similar species. *Sydowia* 60 (1): 41–56.

- Guzmán-Dávalos, L., Mueller, G.M., Cifuentes, J., Miller, A.N. & Santerre, A. (2003) Traditional infrageneric classification of *Gymnopilus* is not supported by ribosomal DNA sequence data. *Mycologia* 95 (6): 1204–1214. https://doi.org/10.1080/15572536.2004.11833028
- Guzmán-Dávalos, L., Ortega, A., Contu, M., Vizzini, A., Rodríguez, A., Villalobos-Arámbula, A.R. & Santerre, A. (2009) Gymnopilus maritimus (Basidiomycota, Agaricales), a new species from coastal psammophilous plant communities of northern Sardinia, Italy, and notes on G. arenophilus. Mycological Progress 8: 195–205. https://doi.org/10.1007/s11557-009-0591-7
- Hesler, L.R. (1969) North American species of Gymnopilus. Mycologia Memoirs 3. Hafner Publishing Company, New York & London, 1–117 pp.
- Høiland, K. (1990) The genus Gymnopilus in Norway. Mycotaxon 39: 257-279.
- Holec, J. (2005) The genus *Gymnopilus* (Fungi, Agaricales) in the Czech Republic with respect to collections from other European countries. *Acta musei Nationalis Pragae, series b, Historia Naturalis* 61 (1–2): 1–52.
- Karsten, P.A. (1879) Rysslands, Finlands och den Skandinaviska halföns Hattsvampar. Förra Delen: Skifsvampar. Bidrag till Kännedom av Finlands Natur och Folk 32: 1–571.
- Kaur, H., Kaur, M. & Rather, H. (2015) Species of *Gymnopilus* P. Karst. new to India. *Mycosphere* 6 (1): 165–173. http://dx.doi.org/10.5943/mycosphere/6/2/7
- Kirk, P.M., Cannon, P.F., Minter, D.W. & Stalpers, J.A. (2008) Ainsworth & Bisby's Dictionary of the Fungi, 10th edn. CAB International, Wallingford, 771 pp.
- Kühner, R. (1980) Les Hyménomycètes agaricoides. Bulletin Mensuel de la Société Linnéenne de Lyon 49: 1–1025.
- Kummer, P. (1871) Der Führer in die Pilzkunde 1871: 1-146.
- Lange, J.E. (1938) Studies in the Agarics of Denmark. Part XII. Hebeloma, Naucoria, Tubaria, Galera, Bolbitius, Pluteolus, Crepidotus, Pseudopaxillus, Paxillus. *Dansk botanisk Arkiv* 9: 1–104.
- Löytynoja, A., & Goldman, N. (2010) webPRANK: a phylogeny-aware multiple sequence aligner with interactive alignment browser. BMC Bioinformatics 11: 579.
 - https://doi.org/10.1186/1471-2105-11-579

Ludwig, E. (2001) Pilzkompendium. Band 1. Beschreibungen. IHW Verlag, Eching, Germany, 758 pp.

- Maire, R. (1933) *Fungi Catalaunici: Contributions à l'étude de la Flore Mycologique de la Catalogne*. Museu de Ciències Naturals, Barcelona, 120 pp.
- Manjula, B. (1983) A revised list of the agaricoid and boletoid basidiomycetes from India and Nepal. *Proceedings of Indian academy of sciences (Plant Sciences)* 92: 81–213.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, Louisiana, 8 pp. https://doi.org/10.1109/gce.2010.5676129
- Moser, M., Ladurner, H., Peintner, U. & Kirchmair, M. (2001) *Gymnopilus turficola* (Agaricales), a new species from subarctic palsa mires and its phylogenetic relationship based on ITS sequences. *Nordic Journal of Botany* 21: 321–327. https://doi.org/10.1111/j.1756-1051.2001.tb00773.x

Munsell, A.H. (1975) Soil color charts. Musell™, Baltimore.

- Murrill, W.A. (1912) The Agaricaceae of the Pacific Coast II. White and ochre-spored genera. *Mycologia* 4: 231–262. https://doi.org/10.2307/3753448
- Orton, P.D. (1960) New check list of British Agarics and Boleti, part III (keys to Crepidotus, Deconica, Flocculina, Hygrophorus, Naucoria, Pluteus and Volvaria). *Transactions of the British Mycological Society* 43 (2): 159–439. https://doi.org/10.1016/S0007-1536(60)80065-4
- Orton, P.D. (1993) *Gymnopilus* Karsten. *In*: Watling R, Gregory NM, eds. 7/Cortinariaceae p.p. *British fungus flora agarics and boleti*. Royal Botanic Garden, Edinburgh, pp. 58–72.
- Rees, B.J. & Strid, A. (2001) Relationships between Australian and Northern Hemisphere *Gymnopilus* species 1: new species and common misconceptions regarding earlier names. *Australasian Mycologist* 20 (1): 30–49.
- Rees, B.J., Marchant, A.D. & Zuccarello, G.C. (2004) A tale of two species—possible origins of red to purple-coloured *Gymnopilus* species in Europe. *Australasian Mycologist* 21 (3): 102–110.
- Rees, B.J., Zuccarello, G.C. & Orlovich, D.A. (2002) Relationships between Australian and Northern Hemisphere *Gymnopilus* species II. A preliminary phylogeny of species of *Gymnopilus* and related genera based on internal transcribed spacer (ITS) region of ribosomal DNA. *Mycotaxon* 84: 93–110.
- Singer, R. (1951) The Agaricales in modern taxonomy. Lilloa 22: 1-832.
- Singer, R. (1962) Diagnoses fungorum novorum Agaricalium II. Sydowia 15: 45-83.

Singer, R. (1986) Agaricales in modern taxonomy. Koeltz, Koenigstein, 981 pp.

- Thomas, A.K., Guzmán-Dávalos, L. & Manimohan, P. (2003) A new species and new records of *Gymnopilus* from India. *Mycotaxon* 85: 297–305.
- White, T.J., Bruns, T.D., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In*: Innis, M.A., Gelfand, D.O., Sninsky, J.J. & White, T.J. (Eds.) *PCR protocols: a guide to methods and applications*. Academic Press, San Diego. pp. 315–322.
 https://doi.org/10.1016/b078-0.12.272180-8.50042-1

https://doi.org/10.1016/b978-0-12-372180-8.50042-1