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Phylogenetic Analysis and Taxonomic Re-evolution of *Geopora foliacea* (Pyronemataceae) in Türkiye

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Abstract

Aim of study: This manuscript aims to contribute to Türkiye's mycobiota by presenting a member of Pyronemataceae whose taxonomic position has been documented by morphological and molecular data.

Area of study: The fungal specimens of the study were collected in the coniferous forest of Genç (Bingöl).

Material and method: The samples were subjected to comprehensive analysis, incorporating morphological evaluation and DNA sequencing of the nrITS region. This process encompassed the examination of both micro- and macromorphological characters to perform phylogenetic analysis.

Main results: The field and two-stage (morphological/phylogenetic) laboratory investigations have revealed that *Geopora foliacea* (Schaeff.) S. Ahmad, belonging to the family P*yronemataceae*, is reported from Türkiye for the first time.

Research highlights: This study introduces ectomycorrhizal *Geopora foliacea*, recorded for the first time in Türkiye. This adds to the previously described genus *Geopora* in Türkiye and increases the number of species to seven.

Keywords: *Ascomycota*, DNA, New Record, Türkiye

Türkiye'deki *Geopora foliacea*'nın (Pyronemataceae) Filogenetik Analizi ve Taksonomik Değerlendirmesi

Öz

Çalışmanın amacı: Bu metnin asıl amacı morfolojik ve moleküler verilerle taksonomik pozisyonu belgelenmiş bir Pyronemataceae üyesi sunarak, Türkiye mikobiotasına katkı sağlamaktır.

Çalışma alanı: Bu çalışmaya ait mantar örnekleri materyalleri Genç (Bingöl) konifer ormanında toplanmıştır.

Materyal ve yöntem: Örnekler, morfolojik değerlendirme ve nrITS bölgesi DNA dizilimi kullanılarak detaylı incelenmiştir. Bu süreç, filogenetik analiz gerçekleştirmek için mikro- ve makromorfolojik karakterlerin incelenmesini içermektedir.

Temel sonuçlar: Arazi ve iki aşamalı (morfolojik/filogenetik) gerçekleştirilen laboratuvar incelemeleri sonucunda *Pyronemataceae* familyasına ait *Geopora foliacea* (Schaeff.) S. Ahmad Türkiye'den ilk kez rapor edilmiştir.

Araştırma vurguları: Bu çalışma, Türkiye'de ilk kez kaydedilen ektomikorizal *Geopora foliacea*'yi tanıtmakta ve Türkiye'de daha önce tanımlanmış *Geopora* cinsine katkı sağlayarak tür sayısını yedi'ye çıkarmaktadır.

Anahtar kelimeler: *Ascomycota*, DNA, Yeni Kayıt, Türkiye

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Introduction

The main ascomata of the *Pezizomycetes*, represented by more than 22 families and a single order (*Pezizizales*), are apothecia. The members of this class can vary in size from a few millimeters to about 20 centimeters. They may have a stalked or sessile cap structure or vary from stipitate to piliate structures, as found in *Discinaceae*, *Helvellaceae*, and *Morchellaceae*. They usually have pigmented ascomata, especially hymenium. Carotenoid pigments are usually characterized, but pigments that can give hymenium brown, orange, purple, or black colors are also present (Pfister & Healy, 2021). Estimated to have originated approximately 400 to 540 million years ago, the class *Pezizomycetes* represents, together with the *Orbiliomycetes*, one of the major lineages of filamentous Ascomycota (Beimforde et al., 2014; Shen et al., 2020). Since identifying unresolved lineages with the application of molecular methods is still ongoing, the diversity of *Pezizales* has not yet been thoroughly documented.

Ascomycota's orders, which have approximately 200 genera and 2000 species, can be epigeous (aboveground) or hypogeous (underground) (Alvarado et al., 2016; Pfister & Healy, 2021). *Pyronemataceae* is the most prominent family of *Pezizales*, comprising 78 genera and approximately 660 described known species, exhibiting highly morphologically and ecologically diverse (Kirk et al., 2008; Hansen et al., 2013). *Geopora* Harkn. is a genus of the family *Pyronemataceae* and was first described by Harkness (1885) for the species *G. cooperi* Harkn. Schäffer described the material of this study as *Elvela foliacea* (1774), *Aleuria foliacea* by Gillet (1879), and *Sepultaria foliacea* by Boudier (1904). Finally, Ahmad (1978) renamed it as *Geopora foliacea* (Schaeff). S. Ahmad. Even though the genus initially encompassed truffle-like species fungi, later, the genus expanded to include hypogean, semi-hypogean, and epigean species with closed or cup-shaped ascocarps. *Geopora* species are distinguished by spherical, semi-spherical, or cup-shaped ascocarps that are wholly or partly hypogean, whitish, grey or yellowish-grey hymenium, eight-spore, operculate, and cylindrical ascus. They also have hyaline paraphyses, usually bifurcated and septate, and the ascospores are ellipsoid, smooth, and often contain one or two large oil drops with smaller oil drops (Grupe et al., 2019; Uzun & Kaya 2019). The genus, represented by 30 species described worldwide (Kirk et al., 2008), is represented by six species in Türkiye (Uzun, 2023). *Geopora arenicola* (Lév.) Kers, *Geopora arenosa* (Fuckel) S. Ahmad, *Geopora clausa* (Tul. & C. Tul.) Burds., *Geopora cooperi* Harkn., *Geopora sepulta* (Fr.) Korf & Burds, and *Geopora sumneriana* (Cooke) M. Torre described from Türkiye using morphological methods. There are no studies focused on *Geopora* phylogeny in Türkiye.

In this study, based on morphological and molecular characters, fungal lists published by Sesli et al. (2020) and Uzun (2023) and some recent studies on Ascomycata (Dizkirici & Acar, 2022; Acar, 2023; Akçay et al., 2023; Acar & Karabıyık, 2024a, Acar & Karabıyık, 2024b; Doğan et al., 2024; Kesici et al., 2024; Terman et al., 2024a; Terman et al., 2024b), it was determined that *Geopora foliacea* is a new record for the mycobiota of Türkiye. Morphological comparison coupled with phylogeny was carried out to determine the classification of the new collection. Internal transcribed spacer (ITS) is used to identfy species molecularly due to its easy amplification, availability of many sequences in the NCBI database and appropriate large barcode gap (Schoch et al., 2012). This region primarily preferred for fungal molecular identification (Tekpinar & Kalmer, 2019).

This study aims to determine the taxonomic position of *Geopora foliacea* within its genus by using macro- and micromorphological features and rDNA internal transcribed spacer (ITS) sequence data and to contribute to the mycobiota of Türkiye.

Material and Methods

The specimens examined in this study were collected from a coniferous forest in the Genç district of Bingöl on March 22, 2018. *Geopora* specimens collected from their natural habitats were identified and classified using an integrated approach combining traditional methods and advanced molecular techniques. The species' taxonomic characteristics (macro and micro characters) were examined in detail, and ITS gene sequences and phylogenetic analyses were evaluated comparatively.

Morphological Studies

Macrofungus specimens collected in the coniferous forest of Genç (Bingöl) were photographed and documented with a Canon 60D digital camera. In addition, all macroscopic data (location collection, date, substrate) were meticulously recorded in the field notebook. After the fieldwork, the *Geopora* specimens were transported to the laboratory, where they were dried under suitable conditions, placed in polyethylene bags, labelled, and turned into fungarium material for further examination. Leica DM500 (Germany) light microscope was used for microscopic examinations. Microscopic characters such as asci, ascospores, paraphyses, and hairs were measured at least 30 times under the microscope of the Leica Application Suite (version 3.4.0) program to ensure that the largest and smallest dimensions were within reliable ranges. In addition, CorelDRAW (64-bit) (Canada) drawing programme was used to ensure accuracy and clarity in depicting the observed micro characters of *G. foliacea*. The macro/micro morphology of the studied specimens was estimated following the literature described by Yao and Spooner (1996a), Ahmad (1978), Tamm et al. (2010), Peric (2011), and Jarjees et al. (2023). After the identification process, the specimens, which were transformed into fungarium material, were preserved and stored under appropriate conditions in the Fungarium of the Department of Biology, Faculty of Science, Van Yüzüncü Yıl University.

Molecular Studies

Total DNA was isolated from dried ascomata utilizing a modified CTAB method (Doyle & Doyle, 1987). The ITS region was amplified using the primer pair N-nc18S10/C26A (Wen & Zimmer, 1996) through polymerase chain reaction (PCR). The amplification process was conducted in a total volume of 25 µl, which included $MgCl_2$ (25 mM), 10X PCR Buffer, dNTP mixture (10 mM), the selected primer pair (10 µM), genomic DNA (10 ng/µl), Taq polymerase (5u/µl) and sterile water. The PCR condition was as follows: an initial denaturation at 95°C for 3 minutes, followed by 35 cycles consisting of denaturation at 94°C for 40 seconds, annealing at 52°C for 30 seconds, and extension at 72°C for 40 seconds, concluding with a final extension at 72°C for 5 minutes. The resulting amplicons were analyzed using 1% TAE agarose gel staining with Gelred dye, and positive results were sequenced in both directions with the same primer using ABI 3730XL automated sequencer (BM Labosis Inc., Ankara, Türkiye). The newly obtained sequence was submitted to GenBank, and an accession number (PV089059) was obtained.

The sequences were analyzed using Finch TV (http://www.geospiza.com/finchtv/) and one reliable sequence was generated by assembling forward (F) and reverse (R) sequences in MEGA v7 (Kumar et al., 2016) with the ClustalW algorithm (Thompson et al., 1994). This sequence was subjected to BLAST analysis in the GenBank database (http://www.ncbi.nlm.nih.gov/) to see closely related taxa and select representative sequences (Appendix 1). *Tricharina gilva* (JQ824118) and *T. ochroleuca* (JQ836558) were selected as the outgroup taxon. Phylogenetic tree inferences were performed with Maximum Likelihood (ML) and Bayesian Inference (BI) methods. ML is a practical method and find the best evolutionary tree by calculating probabilities for character changes. The statistical support ratio of branches in the trees is analyzed with bootstrap (Felsenstein, 1985). ML analysis was performed with IQ-TREE v.1.6.12 (Nguyen et al., 2015) using JC+I+G model of evolution. Branch support was obtained through 1000 replicates of ultrafast bootstrap (UFBoot) (Hoang et al., 2018). Bayesian inference (BI) is a character-based method which employs a likelihood function to get the posterior probability of trees. BI techniques have become very popular in phylogenetics because of the relative ease with which these techniques allow biologists to infer evolutionary patterns using complex and realistic models (Ronquist, 2004). A Bayesian Inference (BI) phylogenetic tree was constructed based on the GenBank database's newly produced and downloaded sequences using MrBayes v.3.2.6 (Ronquist et al., 2012). Two runs with four chains of MCMC iterations were performed for 5 million generations when the average standard deviations of split frequencies were <0.01 (the first 25% of generations were treated as burn-in). A majority rule consensus tree of the remaining trees was calculated. Branch

support was determined by Bayesian Posterior Probabilities (BPP). The tree was visualized using Figtree 1.4.3 (Rambaut, 2018).

Results

The phylogenetic and morphological identification of the collected fungi as *Geopora foliacea* is presented based on the taxonomic keys in scientific references. This includes a brief description of the specimen, macromorphological pictures, micromorphological drawings, location and date, ITS rDNA gene sequence (PV089059), and phylogenetic analysis.

Morphological Taxonomy

Ascomycota Caval.-Sm.
Pezizomycetes O.E. Erikss. & Winka
Pezizales J. Schröt.
Pyronemataceae Corda
Geopora Harkn.
Geopora foliacea (Schaeff.) S. Ahmad (Figure 1–3)

Apothecia 20–50 mm wide, wholly immersed in the soil, and when ripe, appear as a hole with a cracked margin, forming a distinct opening in the soil surface. The inner surface is smooth, pale, light cream to beige color. The outer surface is a typical *Geopora*: velvety, brown, and hairy. Hairs up to 10 µm wide, thick-walled, hyaline to brownish, septate. Asci (190–)200–235 × 16–21.8 µm, hyaline, cylindrical, inamyloid, 8-spored. Ascospores 24.5–28(–30) × (14–)15.8–17.7(–18.5) µm, (n= 30), hyaline, ellipsoid, thick-walled and with a large oil droplet. Paraphyses up to 10 µm wide, sometimes slightly longer than the asci, hyaline, septate, cylindrical with tiny oil droplets. Ectal excipulum up to 40 µm, composed of hyphae in a more or less globose shape, occasionally rectangular.

Specimens examined: Türkiye, Bingöl, Genç Conifer Forest, 38° 44′ 35"N, 40° 34′ 14"E, 1156 m, under *Pinus* sp. trees, wholly immersed in the soil, 22.03.2018, Acar 985.

Figure 1. *Geopora foliacea* a–b. Ascomata

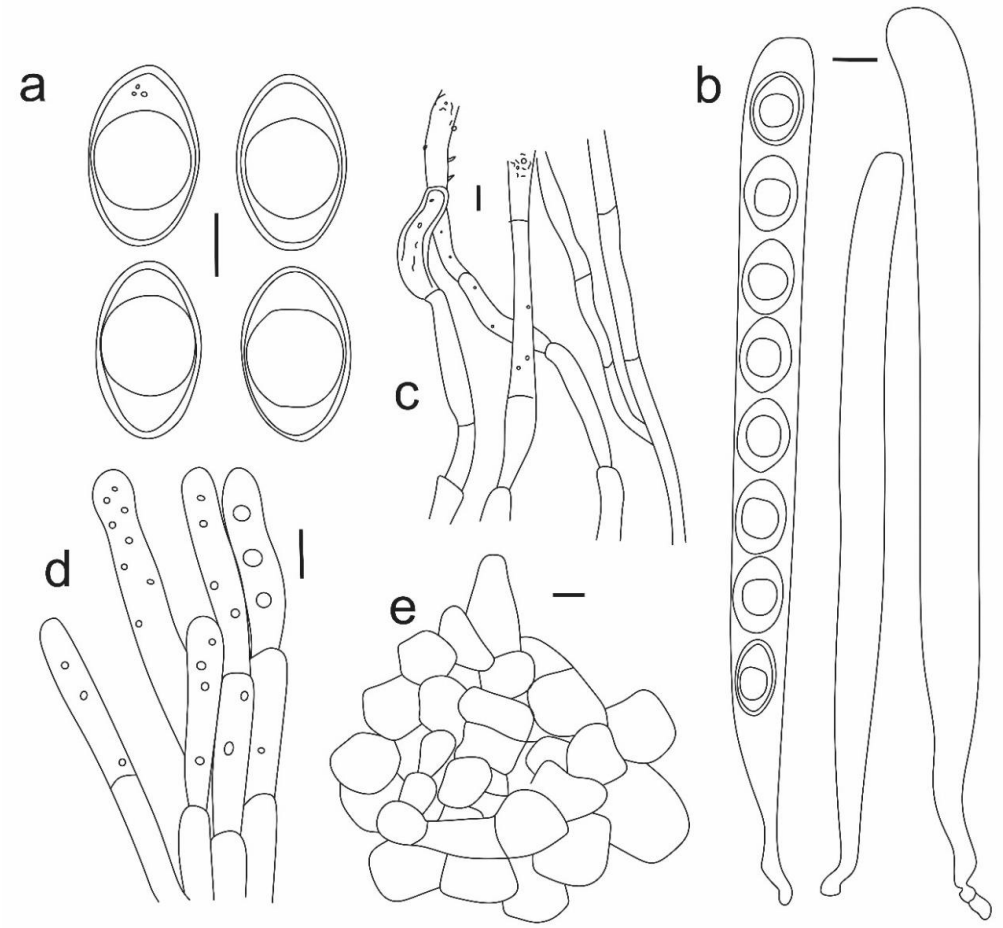

Figure 2. *Geopora foliacea* a. Ascospores, b. Asci, c. Hairs, d. Paraphyses, e. Ectal excipulum Scale bar: 10 µm

Phylogenetic Results

For the first time, the DNA sequence of ITS was generated and used for molecular identification of *Geopora foliacea* taxon in Türkiye. The length of the newly generated sequence was 560 bp after trimming the terminal regions of the aligned F and R sequences. In addition to the generated sequence (GenBank accession number: PV089059), 40 sequences (including 2 outgroups) were downloaded from GenBank, and a total of 41 sequences were analyzed. The aligned ITS data consisted of 614 characters, of which 352 were constant, and 261 were variable (outgroups were not included). The length of the downloaded sequences varied from 418 bp (*Geopora foliacea;* JN812046-JN812048, and ON667912) to 709 bp (MK359200 and MK359201). Nearly the same number of variations were observed in the ITS1 (134) and ITS2 (127) subregions, while no variation or indel was detected in the 5.8S subregion.

The variations were generally caused by a single substitution and/or indel(s) found in different sequences of a single species, so most substitutions were characteristic of only one taxon. For instance, a C-T substitution at position 55, a single base insertion (T) at position 216, a G-C (T or A) substitution at position 444, a G-C (A) substitution at position 501, and a T-C substitution at position 523 were significant variations in the aligned data for identifying species *Geopora foliacea.* The newly generated sequence showed 99.28% homology with *G. foliacea* (JN812046; Kaounas et al., 2011) retrieved from the database. Six nucleotide variations were seen between the studied and downloaded sequences of *G. foliacea*. These variations were observed at positions 113 (G-C), 412, and 420 (C-T), 476 (G-T), 543 (T-C), and 545 (C-T). A total of 46 variations were detected between *G. foliacea* and one of its closest relatives, *G. sepulta.* Most of these variations (31 out of 46) were found in the ITS2 subregion, which was very useful for

phylogenetically differentiating *G. foliacea* from *G. sepulta*.

The phylogenetic tree comprised 41 sequences, representing 12 *Geopora* species and two outgroup taxa from one of the closest genera, *Tricharina*. The tree clearly comprised three well-supported clades (Figure 3). In the first clade, species *G. cooperi*, *G. tolucana*, *G. sinensis*, and *G. lateritia* grouped with strong support (BPP=1.0). *Geopora cercocarpi* formed a well-supported sister group to the *G. arenicola* lineage in the second clade (BS=100, BPP=0.99). Two clusters were observed in the third clade; most of the *G. cervina* samples, *G. tenuis*, and *G. ramila* clustered separately with strong support in the first cluster (BS=87, BPP=1.0) and *G. pinyonensis* located as a distinct lineage. *Geopora foliacea* showed close phylogenetic relationships with *G. sepulta* in the second cluster (BS=98, BPP=1). The newly sequenced *G. foliacea* sample was strongly placed within the *G. foliacea* sub-cluster (BS=100, BPP=1.0), reinforcing the genetic similarity between the Turkish specimen and other *Geopora foliacea* samples.

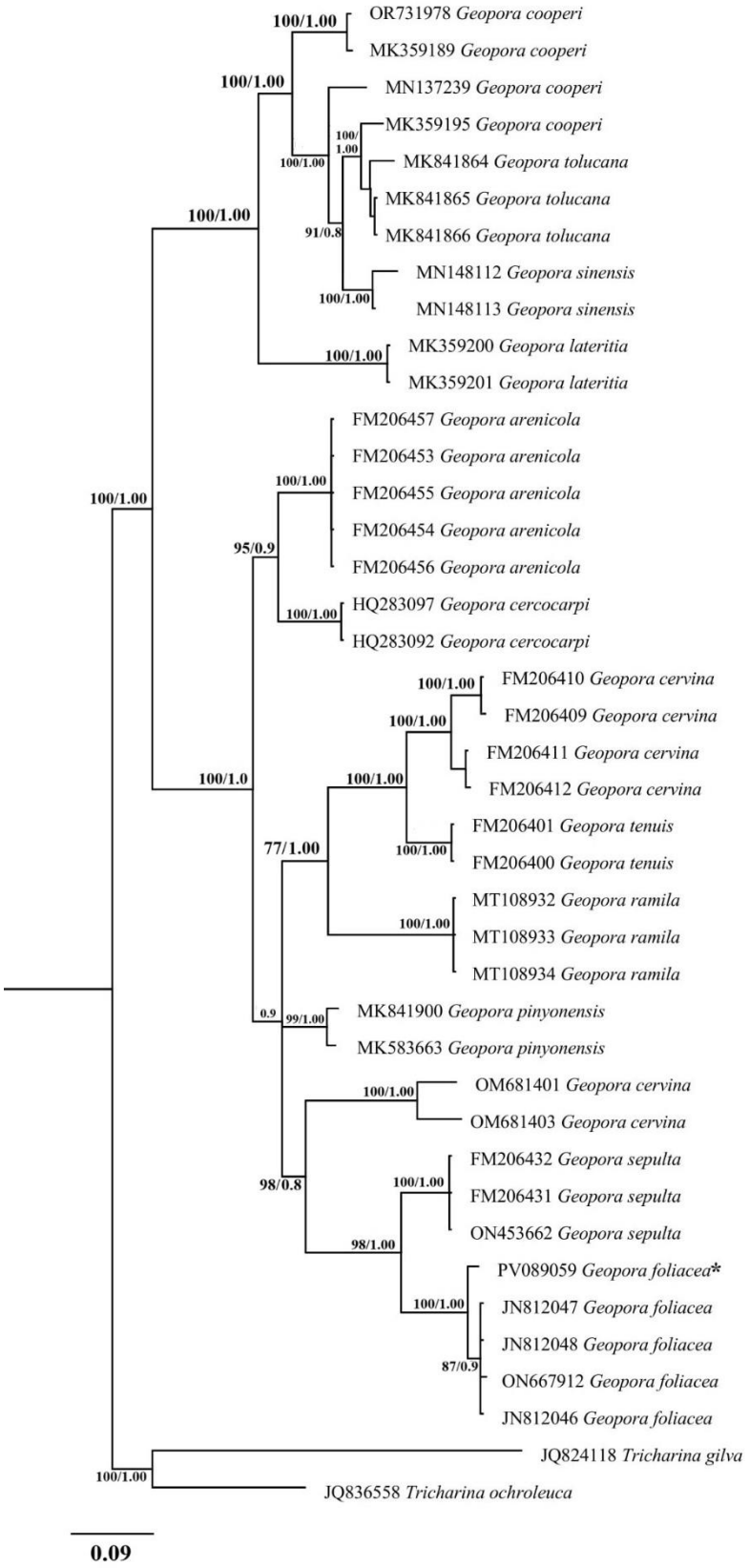

Figure 3. Phylogram derived from BI and ML analysis of the ITS regions. The newly recorded taxon is showing with asterisk. Bayesian posterior probabilities and Bootstrap support values ≥ 50 % are shown.

Discussion

In the most comprehensive phylogenetic study of the *Geopora* genus by Tamm et al. (2010), significant differences were observed in the size of asci and ascocarps between the *G. foliacea* specimens described by Yao and Spooner (1996a) and Ahmad (1978). Yao & Spooner (1996a) reported that *G. foliacea* specimens were similar to *G. cervina* (Velen.) T. Schumach., while Ahmad (1978) reported that the ascocarp of *G. foliacea* specimen reached up to 8 cm. Tamm et al. (2010) reported that neither researcher examined the type specimen and reached a confusing conclusion. Maletti and Ferrari (2016) mentioned that *G. foliacea* can be morphologically confused with *G. arenicola* (Léveillé) Kers and *G. arenosa* (Fuckel) S. Ahmad. Sheibani and Jamali (2020) published a new species, *Geopora ramila* S. Jamali & M. Sheibani and they reported that their species has an apothecium similar to *G. foliacea*, *G. tenuis* (Fuckel) T. Schumach. and *G. cervina* and therefore can be confused with these species. All this complexity within the genus may result from careless examination of phenotypic characters and micromorphological features. In Türkiye, the records of *G. arenicola* and *G. arenosa* specimens have been morphologically described, but no molecular-based study has been carried out yet. In order to clarify the taxonomic confusion and be more reliable, we suggest that morphological and molecular-based studies be conducted to reassess the *Geopora* specimens in fungariums.

The borders of the *Geopora* genus in Türkiye is not exactly known. Therefore, more studies are needed to determine new records and/or new species of the genus in Türkiye. We provided detailed descriptions of *Geopora folicea* and reported based on morphological and molecular characters in the study.

In the produced ITS phylogenetic tree, the newly recorded *G. foliacea* species showed a close relationship with *G. sepulta* downloaded from the database. These two species can be easily distinguished using the micromorphological features of *G. sepulta* [(Asci: 300–360 x 17.0–21.0(–26.0), ascospores: (22.0–)24.0–27.5(–30.0) x 15.0–18.0), Yao & Spooner, 1996b]. *Geopora foliace*, whose potential ectomycorrhizal association with various conifers and deciduous trees was reported by Maia et al. (1996), is widespread in the coniferous forest of Genç (Bingöl).

As a result of this study, the taxonomic position of *G. foliacea* within the genus was determined by using macro/micro characters and ITS sequence data, and the number of species belonging to the genus *Geopora* was increased to seven by contributing to the diversity of the genus in Türkiye.

Ethics Committee Approval

N/A

Peer-review

Externally peer-reviewed.

Author Contributions

Conceptualization: A.D., İ.A. and A.K.; Investigation: A.D., İ.A. and A.K.; Material and Methodology: İ.A. and A.K.; Visualization: A.D., İ.A. and A.K.; Writing-Original Draft: İ.A. and A.K.; Writing-review & Editing: A.D. and İ.A. All authors have read and agreed to the published version of the manuscript.

Conflict of Interest

The authors declare that they have no conflicts of interest.

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Appendix 1

Geopora arenicola (FM206457), Geopora arenicola (FM206453), Geopora arenicola (FM206454), Geopora arenicola (FM206456), Geopora arenicola (FM206455), Geopora cercocarpi (HQ283097), Geopora cercocarpi (HQ283092), Geopora cervina (OM681401), Geopora cervina (OM681403), Geopora cervina (FM206410), Geopora cervina (FM206409), Geopora cervina (FM206411), Geopora cervina (FM206412), Geopora cooperi (OR731978), Geopora cooperi (MN137239), Geopora cooperi (MK359195), Geopora cooperi (MK359189),Geopora foliacea (JN812047), Geopora foliacea (JN812048), Geopora foliacea (ON667912), Geopora foliacea (JN812046), Geopora lateritia (MK359200), Geopora lateritia (MK359201), Geopora pinyonensis (MK841900), Geopora pinyonensis (MK583663), Geopora ramila (MT108932), Geopora ramila (MT108933), Geopora ramila (MT108934), Geopora sepulta (FM206432), Geopora sepulta (FM206431), Geopora sepulta (ON453662), Geopora sinensis (MN148112), Geopora sinensis (MN148113), Geopora tenuis (FM206401), Geopora tenuis (FM206400), Geopora tolucana (MK841864), Geopora tolucana (MK841865), Geopora tolucana (MK841866), Tricharina gilva (JQ824118), Tricharina ochroleuca (JQ836558)