Taiwania 71(3): 435–443, **2026**
DOI: 10.6165/tai.2026.71.435

Abrothallus henryanae (Dothideomycetes: Abrothallales), a new species of lichenicolous fungi on *Sticta henryana* from Arunachal Pradesh, India

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(Manuscript received 4 October 2025; Accepted 27 April 2026; Online published 20 May 2026)

ABSTRACT: A lichenicolous fungus, *Abrothallus henryanae*, is described as new to science, which inhabits the apothecia of *Sticta henryana*. The lichen was collected from Arunachal Pradesh, India. The novel taxon is readily distinguished in having black, stipitate ascomata, covered by greenish-yellow pruina and two-septate, brown, finely ornamented ascospores. The novelty of the species is also confirmed through phylogenetic analyses of the internal transcribed spacer of the ribosomal DNA (nrITS) region. This is the first molecular study of lichenicolous fungi from India. A key to all known lichenicolous *Abrothallus* species colonizing *Sticta* in the world is also provided.

KEY WORDS: *Abrothallus granulatae*, Himalayas, mycobiota, molecular systematics, Northeast India, nrITS, phylogeny.

INTRODUCTION

Lichenicolous fungi represent an evolutionarily successful group of fungi that establishes complex associations with lichens as parasites, broad-spectrum pathogens, saprotrophs or commensals (Diederich *et al*., 2018). *Abrothallus* De Not. is a cosmopolitan genus of lichenicolous fungi predominantly inhabiting foliose and fruticose lichens. The genus was established by G. de Notaris in 1846 (De Notaris, 1846; Suija *et al*., 2024) and it is characterized by black, globose to convex ascomata, usually covered with yellowish or greenish pruina, branched and anastomosed interascal filaments, 4–8-spored asci and 1–3 transversely septate, brown, ornamented ascospores. The majority of the species of *Abrothallus* are known by their sexual morph while some are known solely by their anamorphic stage. *Abrothallus* occurs on a wide range of lichens belonging to Parmeliaceae, Peltigerales, *Ramalina* (Ramalinaceae) and *Cladonia* (Cladoniaceae). Based on multi-locus analyses, Pérez-Ortega *et al*. (2014) provided the first phylogenetic placement of *Abrothallus* within Dothideomycetes and established the new order Abrothallales and family Abrothallaceae. Utilizing two-gene phylogenetic analyses Suija *et al*. (2015) presented an overview of lichenicolous fungi associated with Peltigerales. Their study led to the lectotypification of *A. welwitschii* Mont. ex Tul. and proposal of new combinations for *Vouauxiomyces brattii* S.Y. Kondr. [as *A. brattii* (S.Y. Kondr.) Suija & Pérez-Ort.] and *Epinephroma kamchaticum* Zhurb. & Stepanch. [as *A. kamchaticus* (Zhurb. & Stepanch.) Pérez-Ort. & Suija]. Suija *et al*. (2024), utilizing morphological and molecular characters described three new species (*A. diederichii* Suija & F. Berger, *A. epiclathratus* Suija, Etayo & Flakus, *A. nitassinan* Arsenault, P. Baines & Suija) associated with Peltigeraceae and Pannariaceae. In addition, *A. puntilloi* Brackel was synonymized under *A. lobariae* (Diederich & Etayo) Diederich & Ertz. To date 59 species of *Abrothallus* are recognized worldwide (Index Fungorum, accessed 15 September 2025); among them 21 occur on Pannariaceae (*Erioderma*, *Psoroma*) and Peltigeraceae (*Crocodia*, *Lobaria*, *Lobariella*, *Nephroma*, *Pseudocyphellaria*, *Ricasolia*, *Sticta*) as hosts.

From India four species of *Abrothallus* are known so far, namely *A. peyritschii* (Stein) I. Kotte on *Vulpicida pinastri* (Scop.) J.E. Mattsson & M.J. Lai (Himachal Pradesh; Alstrup and Ahti, 2007), *A. parmeliarum* (Sommerf.) Arnold on *Parmelia squarrosa* Hale (Sikkim; Joshi *et al*., 2016a), *A. microspermus* Tul. on *Flavoparmelia caperata* (L.) Hale, *Punctelia neutralis* (Hale) Krog (Uttarakhand, Arunachal Pradesh; Joshi *et al*., 2018; Jammu and Kashmir; Kumar *et al*., 2022) and *A. welwitschii* Mont. ex Tul. on *Sticta fuliginosa* (With.) Ach., *Sticta platyphylloides* Nyl. [= *Dendriscosticta platyphylloides* (Nyl.) B. Moncada & Lücking (Tamil Nadu, West Bengal; Joshi *et al*., 2018)].

India is a megadiverse country and harbours a rich lichen flora with 3,236 taxa across 487 genera and 88 families (Sinha *et al*., 2024). However, studies on lichenicolous fungi remain insufficient with only 282 species reported so far (Joshi *et al*., 2024). Arunachal Pradesh (26°28'–29°30'N 91°30'–97°30'E) is the largest state in Northeastern India covering a geographical area of 83,743 km². Further, Arunachal Pradesh is a part of the Himalayan biodiversity hotspot with vegetation ranging from tropical lowland forests to high-altitude alpine habitats, sustaining an extraordinary floristic diversity. During a recent collection of lichens from Mayodia Pass in Lower Dibang Valley district of Arunachal Pradesh, a

few samples of *Sticta* infected with lichenicolous fungi were collected. Detailed morphological observations and molecular phylogenetic analyses revealed them to be a new species of *Abrothallus*. This is a valuable addition to the lichenicolous fungal biota of India.

MATERIALS AND METHODS

Microscopy and morphological observations

The lichen specimens observed in the present study were sampled from a tree during winter (February 2023) and hence the locality Mayodia Pass was covered with snow. The samples with lichenicolous fungi were subsequently stored at -20 °C until further processing. The morphological characters of the lichenicolous fungi were analysed using a stereo-zoom Leica S8APO microscope. For anatomical examination thin freehand sections or squash mounts of ascomata were prepared in water and observed under a Leica DM500 light microscope. Both microscopes were equipped with a digital camera and calibrated digital image-processing software. Sections and squash mounts were treated with 10% potassium hydroxide (KOH; K) for microscopic observation. Lactophenol cotton blue (LCB) was used as a fungal stain while Lugol's iodine (I) was applied directly or after pretreatment with KOH (K/I) to examine amyloid reaction. Measurements were taken in water and ascospore dimensions are represented as (a–)b–c(–d); where b–c represents the mid 90% of values around the mean; 'a' and 'd' within parenthesis denotes the extreme values, followed by the number of observations (n). The identified sample was deposited as a voucher specimen in the herbarium LWG of CSIR-National Botanical Research Institute, Lucknow. Georeferencing of the sampling site was carried out with Google Earth Pro 7.3 and a distribution map was prepared using QGIS 3.10 (Fig. S1).

DNA extraction, polymerase chain reaction and sequencing

About 15–20 apothecia of *Abrothallus* were carefully removed from the lichen using a blade, scalpel or forceps, and washed in double-distilled water to remove surface contaminants (Pérez-Ortega *et al*., 2014). The genomic DNA was extracted using the CTAB method (Doyle and Doyle, 1987). The nuclear ribosomal internal transcribed spacer (nrITS), recognized as the universal fungal barcode (Schoch *et al*., 2012), showing the greatest variability (Suija *et al*., 2015) was amplified using the primers ITS1 and ITS4 (White *et al*., 1990). The PCR reactions and thermal cycles were set according to Nayaka and Debnath (2023). Amplified PCR products were visualized by electrophoresis on a 1% agarose gel stained with ethidium bromide using a gel documentation system under UV light. The purified PCR product was subjected to Sanger sequencing.

Dataset representation

The newly generated sequence data were examined, verified and assembled with BioEdit v7.2.5 (Hall, 1999). The sequence was subjected to Basic Local Alignment Search Tool (BLASTn) search which indicated its affiliation to *Abrothallus*. The sequence was then deposited in NCBI GenBank under the accession number PX108869 (537 bp) (Table S1). For phylogenetic analyses sequences of related taxa with the highest percent identity and query coverage were retrieved from GenBank nucleotide database. A total of 43 nrITS sequences, including the new sequence were selected to build the dataset. These sequences mostly belonged to previous studies on this genus by Suija *et al*. (2015), Flakus *et al*. (2019) and Suija *et al*. (2024). Based on Suija *et al*. (2024) three *Abrothallus* species, viz. *A. acetabuli* Diederich, *A. santessonii* (D. Hawksw.) Suija, D. Hawksw. & Pérez-Ort. and *A. usneae* Rabenh. were selected as outgroup taxa (Table S1). The sequence of *A. macrosporus* (MT153944) generated an anomalous branch in the phylogenetic reconstruction, and therefore was not included in the current study.

Sequence alignment and phylogenetic analyses

A multiple sequence alignment of the nrITS dataset was conducted using MAFFT v7.505 on XSEDE (Katoh and Standley, 2013) with default parameters via the CIPRES Science Gateway v3.3 web portal (Miller *et al*., 2010). The resulting alignment was subsequently imported to AliView v1.17.1 (Larsson, 2014) for trimming of unevenly aligned terminals. The best-fit nucleotide substitution model for Maximum Likelihood (ML) analyses was determined using jModelTest2 (Darriba *et al*., 2012) on ACCESS v2.1.6 through the CIPRES web portal, based on the Bayesian Information Criterion (BIC). Transitional Model 2 (TIM2+I+G), incorporating invariant sites and gamma-distributed rate heterogeneity, was chosen as the best-fit model, showing the lowest BIC value of 7221.804. ML analyses were performed in RAxML-HPC2 v8.2.12 (Stamatakis, 2014) on the CIPRES Science Gateway platform with 1000 bootstrap replicates under the default nucleotide substitution model.

Bayesian inference (BI) analyses were conducted in MrBayes v3.2.2 (Ronquist *et al*., 2012) using the General Time Reversible substitution model with invariant sites and gamma-distributed rate heterogeneity (GTR+I+G). This model was selected as the best-fit substitution model by PartitionFinder based on the lowest AIC value (6732.6499). The BI analyses followed two simultaneous independent runs (nruns=2), using 4 incrementally heated chains (nchains=4) starting from a random tree. The Markov Chain Monte Carlo (MCMC) analyses were run for 2 million generations (ngen=2000000), with sample frequency (samplefreq=200) and print frequency (printfreq=200) for every 200 generations, while convergence

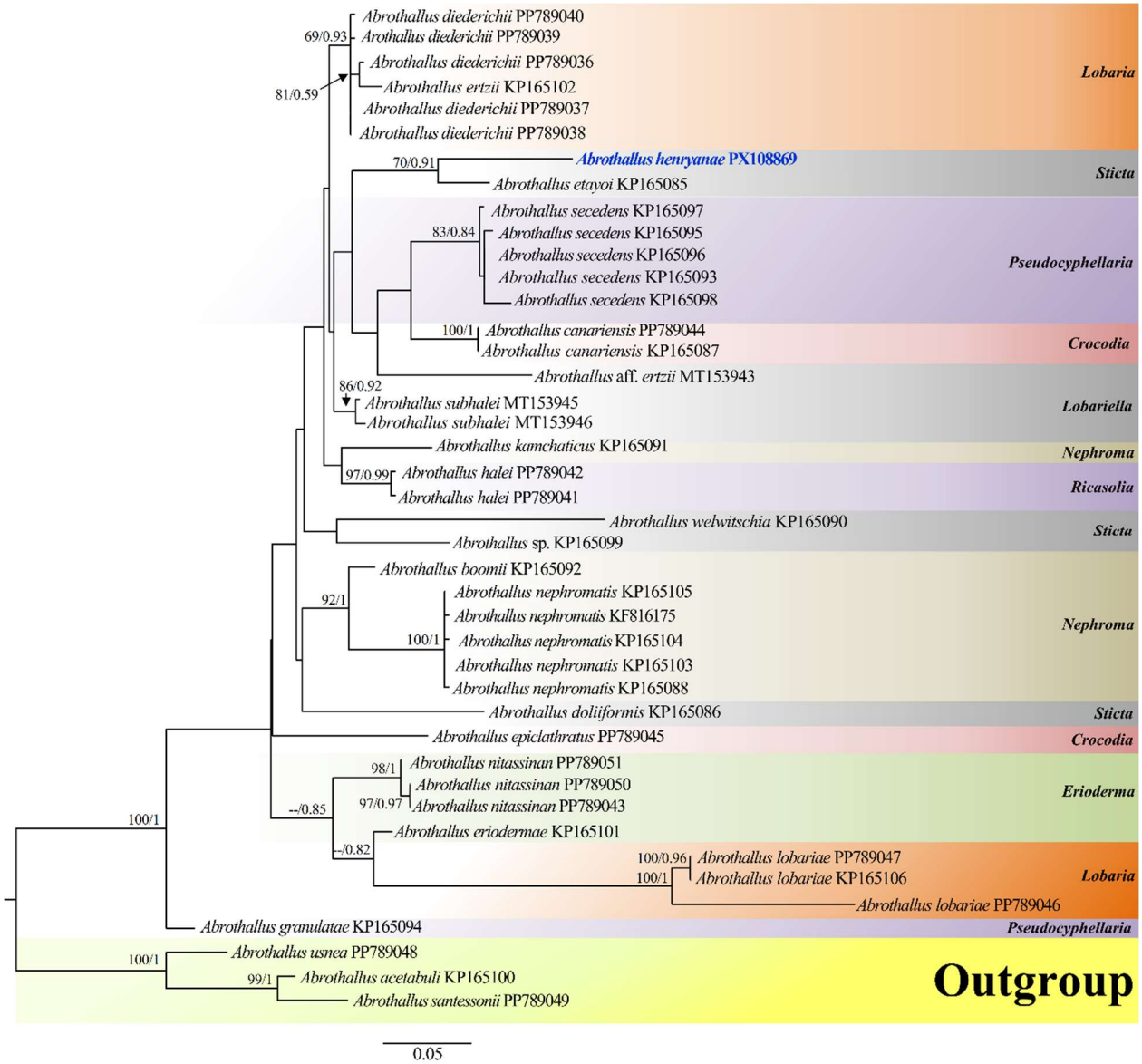

Fig. 1. Maximum likelihood phylogenetic tree constructed from the nrITS sequence data for the genus *Abrothallus* growing on members of Peltigerales. Maximum likelihood bootstrap MLBS ≥ 50% and Bayesian posterior probabilities ≥ 0.50 are indicated in the tree above their corresponding nodes. The scale bar represents the expected number of nucleotide substitutions per site. Newly generated sequence of *A. henryanae* is highlighted in blue and bold font.

diagnostics were assessed every 1000 generations (diagnfreq=1000). The analyses terminated with average standard deviation of split frequencies reaching value of 0.01 and the potential scale reduction factor (PSRF) approaching value 1 at the end of the specified number of generations. The results were summarized using the commands 'sump' and 'sumt'. The initial 25% of sampled trees were discarded as burn-in and a consensus tree was generated from the remaining trees to estimate posterior probabilities (PP) of the group. The generated phylogenetic ML tree and the Bayesian inference tree were finally visualized in FigTree v.1.4.4. (Rambaut, 2014).

RESULTS

The alignment of nrITS sequence data contained 550 characters with 254 distinct alignment patterns and 12.26% undetermined characters. The estimated nucleotide base frequencies were documented as: A = 0.210321, C = 0.324732, G = 0.279716, T = 0.185232; substitution rates: AC = 2.218748, AG = 4.217582, AT = 1.466328, CG = 1.042787, CT = 7.503910, GT = 1.000000. Additionally, alpha = 0.280316 and the tree length = 1.884709.

The phylogenetic tree obtained from ML and BI analyses displayed nearly uniform topology. Therefore, only the optimal ML tree displaying the final optimization likelihood value of -3336.094477 is presented (Fig. 1) with

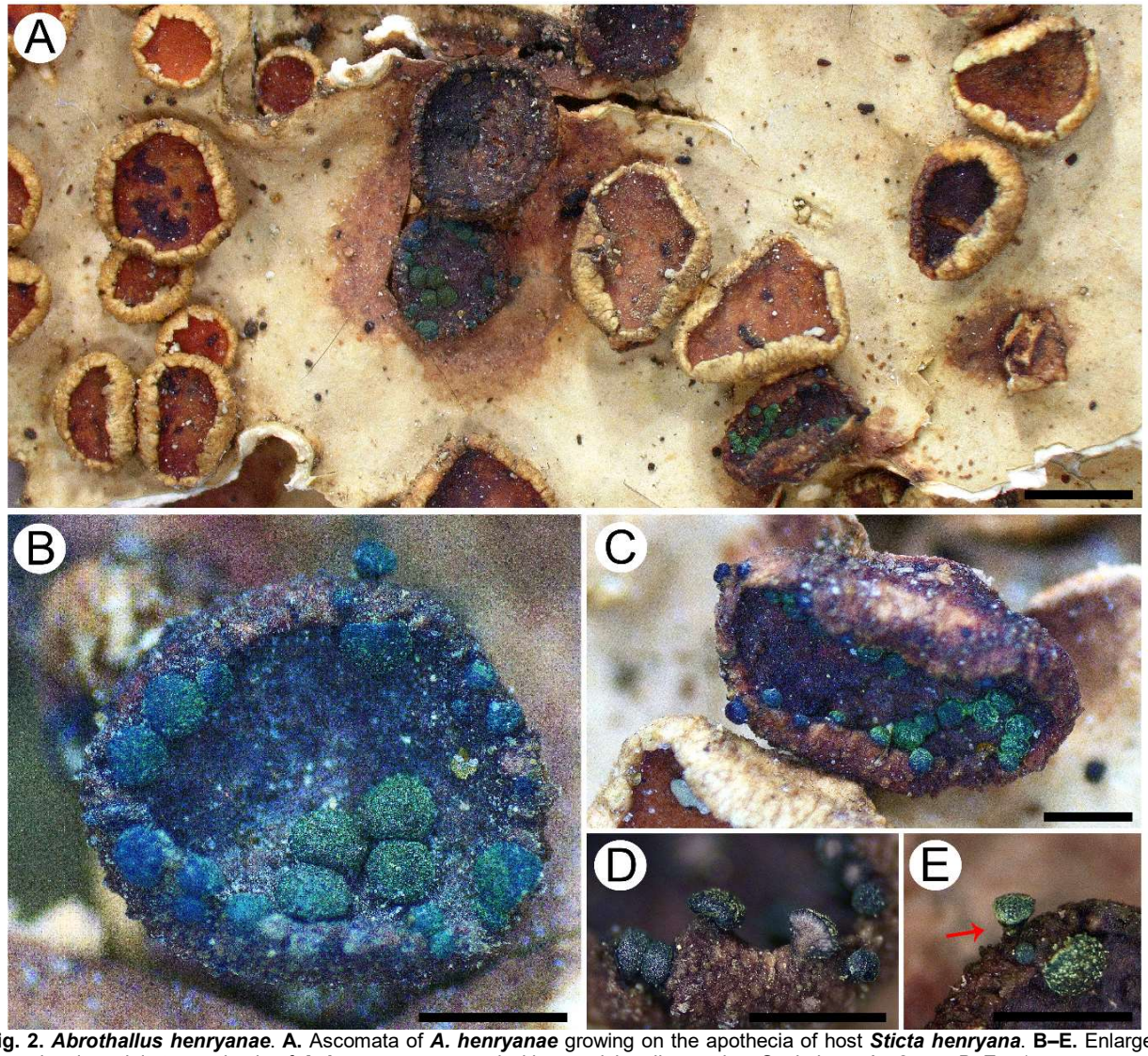

Fig. 2. ***Abrothallus henryanae***. **A.** Ascomata of ***A. henryanae*** growing on the apothecia of host ***Sticta henryana***. **B–E.** Enlarged view showing stipitate apothecia of ***A. henryanae*** covered with greenish-yellow pruina. Scale bars: A= 2 mm; B–E = 1 mm.

branch support values from both ML bootstrap analyses and BI posterior probabilities. The resulting phylogenetic tree is annotated with ML bootstrap values (BS) ≥ 50% and BI posterior probabilities (PP) ≥ 0.50.

The phylogenetic analyses demonstrated that *Abrothallus* species associated with Peltigeraceae and Pannariaceae form a well-supported and distinct lineage. Each lineage corresponds to a morphologically and anatomically well-delimited species. The phylogenetic tree topology obtained in the present study is congruent with Suija *et al*. (2024). ITS data place the new species *A. henryanae* as a sister clade of *A. etayoi* Pérez-Ort. & Suija with a well-supported lineage (MLBS = 70%, PP = 0.91).

TAXONOMIC TREATMENT

Abrothallus henryanae A. Debnath & Nayaka, ***sp. nov.*** **Figs. 2 & 3**

MycoBank: MB 862230; **GenBank nrITS:** PX108869

Type: INDIA, Arunachal Pradesh, Lower Dibang Valley district, Mayodia Pass, 28°14'56.14"N, 95°54'44.37"E, 2655 m a.s.l., on apothecia of *Sticta henryana* Müll. Arg., on tree bark, 17 February 2023, *S. Nayaka and A. Debnath* 23-368319 (LWG, holotype).

Diagnosis: Among *Abrothallus* species on Peltigeraceae and Pannariaceae, *Abrothallus granulatae* is the only species with two-septate ascospores while all other *Abrothallus* species on Peltigeraceae and Pannariaceae have one or three septate ascospores. The new species differs from *A. granulatae* by having well developed stipe, slightly bigger ascospores (8–15 × 3.5–5 vs. 9.5–12 × 4.0–4.5 µm) and different host (*Sticta henryana* vs. *Pseudocyphellaria granulata*).

Description: Appearing as black, yellowish green globular ascomata on dark, necrotic areas of apothecial disc or margin of *Sticta henryana.* **Ascomata** apothecioid,

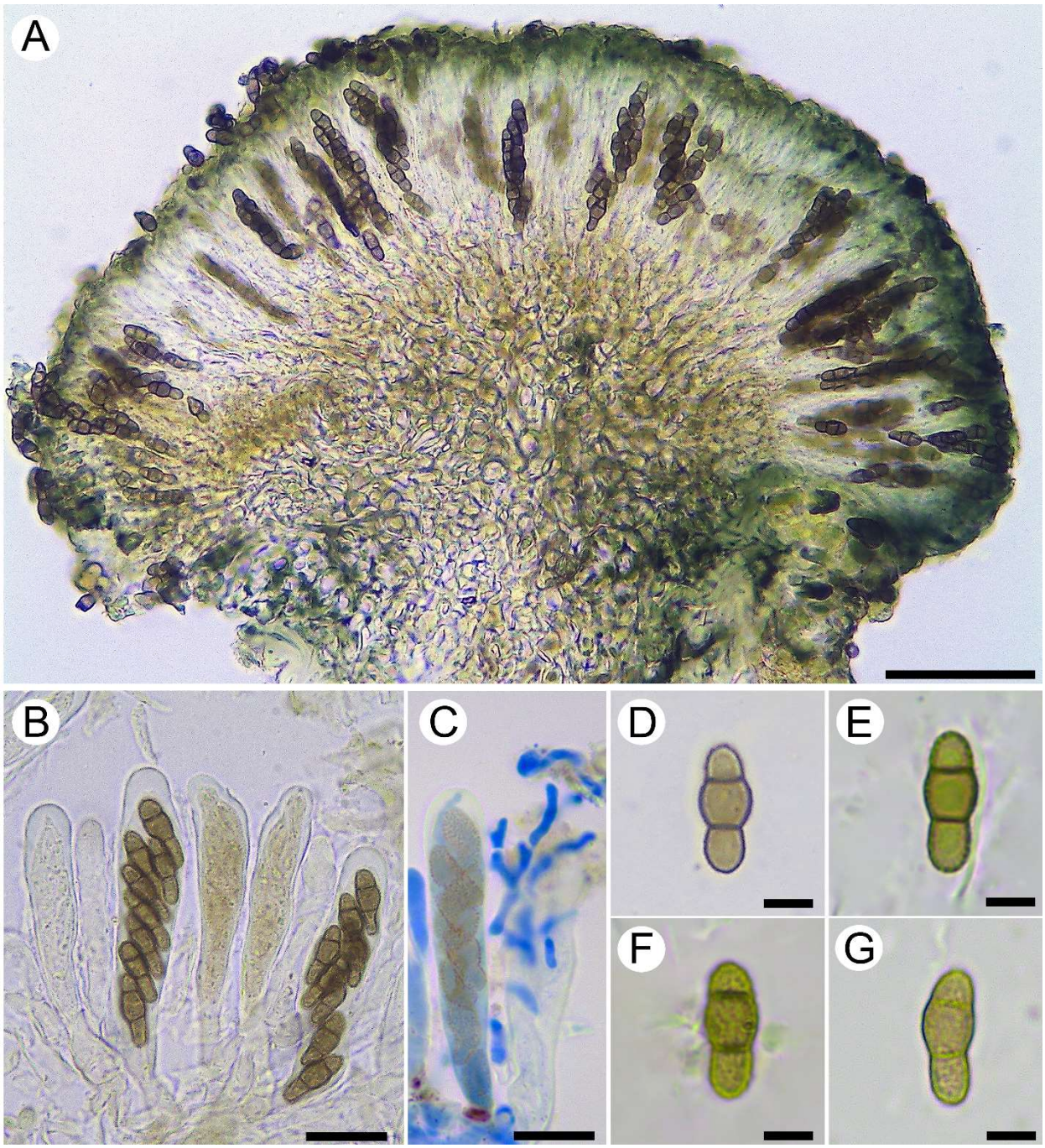

Fig. 3. Anatomical details of ***A. henryanae***. **A.** Cross section of the apothecium, **B–C.** Asci with uniseriately arranged ascospores, D–G. Two-septate, brown, finely ornamented ascospores. Scale bars A= 50 µm; B, C= 20 µm; D–G = 10 µm.

solitary or in groups of 4–5, 0.4−0.6 mm diam., subglobose to lenticular, stipitate; stipe 0.07−0.13 mm tall, blackish-brown; disc, strongly convex, rarely flat, black, with persistent, dense, yellowish green pruina; margin black, thin, disappearing at maturity. **Exciple** poorly differentiated, indistinct, pseudoparenchymatous in section, composed of thin-walled, small, polygonal cells 10−30 µm diam., with a greenish tinge, lacking in mature apothecia, K+ olive-green. **Epihymenium** olive green to olivaceous-brown, 6−8 µm high, K+ greenish, with dark green granules dissolving in K. **Hymenium** hyaline to pale olive green, not inspersed, 40−50 µm tall, I–, K+ green intensified, K/I –. **Subhymenium** inconspicuous, hyaline, 15−20 µm high. **Hypothecium** light brown to green, continuous with the stipe, 100–110 µm thick, composed of polygonal, subpolygonal or subglobose cells, thin-walled cells in section, 6−8 × 4−6 µm. **Interascal filaments** filiform, hyaline, septate,

sparingly to irregularly branched, anastomosing, slightly swollen at the tip, with greenish-brown to olivaceous pigments above, 44−50 × 1.5−2.5 µm. **Asci** fissitunicate, cylindrical to narrowly clavate, stalked, slightly thickened at the apex, having a small apical ocular chamber, 8-spored, uniseriate, 45−57 × 10−12 µm, I–, K/I–. **Ascospores** dark brown, fusiform, 2-septate, constricted at both septa, median cell usually broader and wider, (8–)10–12(–15) × (3.0–)4–4.5(–5) µm, n = 30; ascospore wall finely ornamented and verruculose at maturity.

Etymology: The species epithet '*henryanae*' was derived from the species epithet '*henryana'* of the host lichen.

Habitat and distribution: The new species is currently known only from the type locality Mayodia Pass in Lower Dibang Valley district of Arunachal Pradesh at an elevation 2655 m, found growing only on the apothecia of *Sticta henryana* notably in the area influenced by seasonal snow. *Abrothallus henryanae* is pathogenic as indicated by dark, discoloured patches on apothecia of the host lichen where this fungus grows.

DISCUSSION

Taxonomy: The new taxon differs from all the known *Abrothallus* species in having distinctly stipitate ascomata. Further, it is characterized by 2-septate, brown, fusiform ascospores which do not break into parts and *Sticta henryana* as host. A total of four species of *Abrothallus* are known to colonize *Sticta* – *A. doliiformis* Pérez-Ort. & Suija, *A. etayoi* Pérez-Ort. & Suija, *A. stictarum* Etayo and *A. welwitschii* Mont. ex Tul. Among them *A. doliiformis* and *A. etayoi* are known only by their anamorphic stage; *A. stictarum* has 1–3-septate ascospores; *A. welwitschii* has 1-septate ascospores while *A. henryanae* has 2-septate ascospores. By having 2-septate ascospores and a stipe *A. granulatae* growing on *Pseudocyphellaria granulata* is close to the new species, however, the hosts differ between the two species. Further, ascospores dimensions differ in *A. granulatae* (9.5–12 × 4.0–4.5 vs. 8–15 × 3.5–5 µm) and stipes absent or rarely very short. Geographically, *A. granulatae* is found in Argentina while *A. henryanae* is found in India and both form separate phylogenetic lineages. According to the phylogenetic analyses *A. henryanae* is closely related to *A. etayoi* by forming a well-supported sister clade and growing on *Sticta* hosts, however, no sexual stage is known for the latter. Based on the BLAST analysis the pairwise alignment between *Abrothallus henryanae* (PX108869; 537 bp) and *A. etayoi* (NR_158309.1 = KP165085; 545 bp) showed 359/365 bp identity (98%) with no gaps (0/365 bp). Detailed comparison of *A. henryanae* with other taxa occurring on members of Peltigeraceae and Pannariaceae is given in Table 1.

Ecology and biodiversity: *Abrothallus* is a cosmopolitan taxon occurring on a wide range of hosts belonging to the families Cladoniaceae Zenker, Lobariaceae Chevall., Nephromataceae Wetmore ex J.C. David & D. Hawksw., Pannariaceae Tuck., Parmeliaceae Bercht. & J. Presl, Ramalinaceae C. Agardh and Stereocaulaceae Chevall. Suija *et al*. (2015) observed that despite the considerable global distribution of *Abrothallus*, the sampling has been concentrated mostly in Europe and the Americas, whereas collections from Asia and Africa are limited. In this context the discovery of a new species from India is a significant contribution to the genus. It is interesting to note that *A. henryanae* was collected from a high-altitude habitat covered in snow during the winter. The presence of snow might be ecologically significant as it provides the *Sticta* host with a prolonged source of moisture. Suija *et al*. (2018) described the lichenicolous fungal genus *Taitaia* Suija, Kaasal., Kirika & Rikkinen from cool, persistently moist tropical montane forests at higher elevations in East Africa, where high humidity, low temperature and high elevation favour the establishment of lichenicolous fungi. Zhurbenko (2013) enumerated 36 lichenicolous fungi from Jammu and Kashmir state of India. The collection sites included high altitude and colder areas such as Gulmarg, Khardung-La pass, Pahalgam and Sonmarg. These studies indicate that places with cool, humid environments and high elevation favour the growth of lichenicolous fungi.

Debnath and Nayaka (2023) have recently recorded 903 lichen species from Arunachal Pradesh, characterized by tropical to temperate climate, high rainfall, unique topography and vegetation, making it a lichen diversity hotspot. New or previously undocumented taxonomic novelties are frequently being reported from this region (Debnath *et al*., 2025). However, documentation of lichenicolous fungi has remained limited in the state and previously, only six species were known: *Stigmidium frigidum* (Th. Fr. ex Sacc.) Alstrup & D. Hawksw. on *Thamnolia vermicularis* (Sw.) Schaer. (Joshi *et al*., 2016a), *Didymocyrtis thamnoliicola* Y. Joshi, R. Bajpai & Upreti on *Thamnolia vermicularis* (Sw.) Schaer. (Joshi *et al*., 2016b), *Abrothallus microspermus* Tul. on *Flavoparmelia caperata* (L.) Hale (Joshi *et al.,* 2018); *Laetinaevia epithallina* (W. Phillips & Plowr.) Baral = *Pezizella epithallina* (W.Phillips & Plowr.) Sacc on *Peltigera canina* (L.) Willd. (Joshi *et al*., 2018), *Arthonia coronata* Etayo on *F. caperata* (L.) Hale (Joshi, 2018) and *Didymocyrtis melanelixiae* (Brackel) Diederich, R.C. Harris and Etayo on *Parmotrema saccatilobum* (Taylor) Hale (Sharma *et al*., 2023). This study indicates that further exploration across habitats in the state would result in discovery of more hidden fungal diversity.

World key to the species of *Abrothallus* on lichen genus *Sticta*

1a. Sexual morph present ……..…… 2
1b. Sexual morph absent …….. 4
2a. Ascomata mostly on the host thallus, not shortly stipitate, ascospores 1–3-septate …… 3

Table 1. Comparison of ***Abrothallus henryanae*** with other species colonizing host Peltigerales. "—" means absent or no data available.

Species	Host	Shape of ascomata	Ascocarp position on host	Pruina	Siza of ascomata (mm)	Stipe	Spores per ascus	Spore length (µm)	Spore width (µm)	Septa	Part spores	Asexual morph	Reference
A. boomii	*Nephroma tangeriense*	convex, tuberculate	on thallus	Yes	0.28–0.52	—	(4–)6(–8)	11.5–20.5	5.5–7	1–3	—	immersed to slightly erumpent	Suija *et al.*, 2015
A. brattii	*Pseudocyphellaria faveolata*	—	—	—	—	—	—	—	—	—	—	gall or wart like	Kondratyuk, 1996
A. canariensis	*Crocodia aurata*	superficial, flat	on thallus	Yes	0.27–0.52	—	4–6	16–25	6–9.5	1	Yes	not seen	Suija *et al.*, 2015
A. diederichii	*Lobaria pulmonaria*	strongly convex	on upper cortex	Yes	0.2–0.5	Yes	6–8	(11.2–)12–13.6 (–16)	(3.8–)4.0–4.8(–5.6)	3	Yes	fully immersed	Suija *et al.*, 2024
A. doliiformis	*Sticta* sp.	—	—	—	—	—	—	—	—	—	—	doliiform	Suija *et al.*, 2015
A. epiclathratus	*Crocodia* sp.	superficial, flat	on thallus	No	0.27–0.33	—	4	(15–)15.8–18.3 (–19)	(6.0–)6.7–7.7(–8.0)	1–3	No	not seen	Suija *et al.*, 2024
A. eriodermae	*Erioderma* sp.	convex	on both apothecia and thallus	Yes	0.18–0.54	—	8	9–11.5	3.5–4.5	1	Yes	subglobose to lageniform	Suija *et al.*, 2015
A. ertzii	*Lobaria pulmonaria*	plane to convex	on thallus	Yes	0.14–0.36	—	8	9–11.5	3–4.5	1	Yes	not seen	Suija *et al.*, 2015
A. etayoi	*Sticta* sp.	—	—	—	—	—	—	—	—	—	—	barrel shaped to subglobose	Suija *et al.*, 2015
A. granulatae	*Pseudocyphellaria granulata*	superficial	on thallus	Yes	0.1−0.4	Yes	8	9.5–12	4.0–4.5	1–2	—	partly immersed	Wedin, 1994
A. halei	*Ricasolia quercizans*	convex to plane	on both apothecia and thallus	Yes	0.2–0.55	Yes	(4–)6(–8)	9–(10·7)–14	3·0–(3·0)–4·0	1–3	Yes	not seen	Suija *et al.*, 2010
A. henryanae	***Sticta henryana***	**sub globose to lenticular**	**on apothecia**	**Yes**	**0.4−0.6**	**Yes**	**8**	**(8–)10–12(–15)**	**(3.5–)4–4.5(–5)**	**2**	**No**	**not seen**	**This study**
A. kamchaticus	*Nephroma* sp.	flat to convex	on thallus	Yes	0.25–0.52	—	8	11.5–16	5–7.1	1	—	semi-immersed to slightly erumpent	Suija *et al.*, 2015
A. lobariae = *A. puntilloi*	*Lobaria pulmonaria*	rounded convex	on thallus	Yes	0.1–0.21	—	6–8	(8.5 –)8.9 –10.1(–10.5)	(4.0–)4.1–5.0	1	Yes	completely to half immersed, subglobulose	Brackel and Puntillo 2016
A. macrosporus	*Lobariella crenulata*	plane	on apothecia	No	0.2–0.5	Yes	5–8	18.5–24	7–9	3	No	—	Etayo, 2010
A. nephromatis	*Nephroma parile*	flat	on thallus	Yes	0.27–0.54	—	8	10–(14)–17.8	3.4–(5.4)–7.2	1	No	immersed to erumpent	Suija *et al.*, 2015
A. nitassinan	*Erioderma pedicellatum*	flat to strongly convex	on apothecia	Yes	0.1–0.4	—	8	(9.5–)9.9–12.1(–14.0)	(3.5–)3.5–4.7(–5.5)	1	Yes	immersed	Suija *et al.*, 2024
A. psoromatis	*Psoroma* sp.	—	—	—	—	—	—	—	—	—	—	subglobose to ampulliform or lageniform	Diederich *et al.*, 2018
A. secedens	*Pseudocyphellaria dubia*	immersed to erumpent	on thallus	Yes	0.25−0.4	No	8	12.5–16.0(–17.5)	5.5–6.5(–7.0)	1	Yes	not seen	Wedin, 1994
A. stictarum	*Sticta* sp.	plane-convex	on thallus	No	0.3–0.5	No	8	13.5–18	5–6	1–3	—	semi-immersed	Etayo, 2002
A. subhalei	*Lobariella crenulata*	plane convex to subspherical	on thallus	Yes	0.22–0.45	No	8	9–13	3–5	1–3	No	immersed to slightly erumpent	Flakus *et al.*, 2019
A. welwitschii	*Sticta sylvatica*	flat	on thallus	Yes	0.27–0.72	—	8	12.8–(15)–17.6	4–(6)–7.9	1	No	semi-immersed	Suija *et al.*, 2015

2b. Ascomata only on the host apothecia, shortly stipitate, greenish yellow pruinose, 0.4–0.6 mm diam., ascospores 2-septate, 8–15 × 3.5–5 µm …….. ***A. henryanae***
3a. Ascomata epruinose, flat to convex, 0.3–0.5 mm diam., hymenium violet, ascospores with up to 3 septa, 13.5–18 × 5–6 µm . ***A. stictarum***
3b. Ascomata pruinose, flat, > 0.55 mm diam., hymenium olive green, ascospores 1-septate only, 12.8–17.6 × 4–7.9 µm …… ***A. welwitschii***
4a. Pycnidia semi-immersed 5
4b. Pycnidia superficial 6
5a. Pycnidia 100–150 µm wide, conidia 6–10 × 4–5 µm .... ***A. stictarum***
5b. Pycnidia 130–340 µm wide, conidia 9.6–12.8 × 5.6–7.2 µm .... ***A. welwitschii***
6a. Conidiomata doliiform, 250–450 µm wide, walls composed of 5–8 layers, conidia 9.5–14.5 × 6–9.5 µm …… ***A. doliiformis***
6b. Conidiomata barrel-shaped to subglobose, 220–350 µm wide, walls composed of 7–12 layers, conidia 11–17.5 × 7–11 µm ……. ***A. etayoi***

ACKNOWLEDGMENTS

The authors are grateful to the Director, CSIR-National Botanical Research Institute, Lucknow, for providing essential infrastructure and laboratory facilities; to Anusandhan National Research Foundation (ANRF; formerly Science and Engineering Board, SERB, New Delhi) for financial support under file number CRG/2021/002263 and to the Department of Environment and Forests, Itanagar for granting permission to conduct fieldwork and access forest areas in Arunachal Pradesh. This manuscript has been approved through the institute's Publication Ethics Committee with number CSIR-NBRI_MS/2026/01/07.

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